The ecology of breeding waterfowl at the Ouse Washes, England

G. J. THOMAS

Introduction

Unimproved washland is now a rare ecosystem in Britain. The best example is the Ouse Washes, which is still flooded practically every winter, and holds important populations of wintering wildfowl. (Cadbury 1975; Thomas 1978; Owen & Thomas 1979). The winter floods sometimes persist into the spring and are often supplemented by smaller floods in April and May and exceptionally later. This can result in conditions favourable to breeding waders (Cottier & Lea 1969) and waterfowl. The present account briefly reviews the history of waterfowl on the Ouse Washes from 1968–78 and describes some of their habitat preferences and feeding ecology between 1970–1972. Waterfowl are considered as being ducks, Coot *Fulica atra* and Moorhens *Gallinula chloropus*. Little seems to have been published about waterfowl nesting in washlands and the Ouse Washes populations are compared to what is known about some other flood plain areas in Britain.

Full details of the Ouse Washes are given in Thomas (1978) and a location map is shown in Figure 1. The area is dominated by reed grass *Phalaris arundinacea* and reed sweet grass *Glyceria maxima*. Most of the 1914 ha of fields are grazed each year with some mown for hay. The spring of 1970 was characterized by a May flood over c. 55% of the area which abated in June. There was a smaller flood covering about 24% in 1971 and no flood in the spring of 1972. In all three years there was about 41 ha of permanent water in pools and ditches.

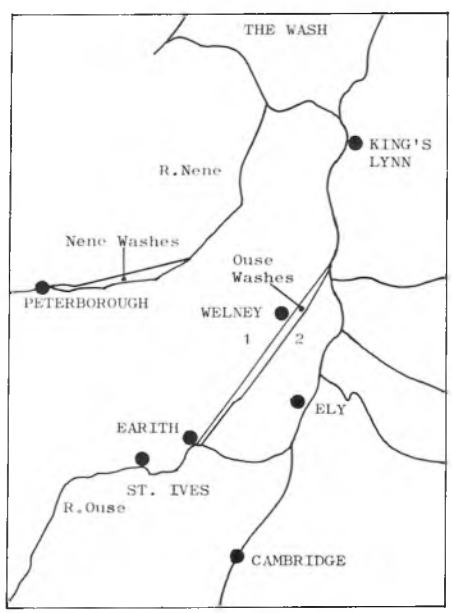

Figure 1. Location map of the Ouse Washes. 1 = Old Bedford River; 2 = New Bedford River.

Materials and methods

Two or three censuses were carries out in April and May between 1970–1972 to determine the breeding populations. For ducks the populations are estimated from an average of the number of males (paired and non-paired) seen. This may have resulted in a slight over-estimate because of an excess of males over females in pre-breeding populations of ducks. (In Holland, Eygenraam (1957) determined a sex ratio of 106 male: 100 female Mallard *Anas platyrhynchos*.) At the Washes the number of females sometimes came close to that of the males but never exceeded it; some of the female Mallard must have been missed because they were incubating. For Moorhen and Coot the total numbers were simply divided by two.

Subsequent censuses were carried out in June and July. These and special watches on pools used by females during incubation and with broods gave a better idea of the breeding populations of the rarer ducks.

In each year the same 582 ha of washes and banks were searched for nests, mainly in May, by a team, usually of 4 people, slowly walking about 15–20 m apart. Nest positions were plotted, the dominant plant at the nest site was identified, and the degree of cover estimated as 0%, 25%, 50%, 75% and full. The height of vegetation at and around the nests was measured, discounting any exceptionally long leaves or stems (sometimes 1–3). Four readings

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were taken around each nest, each 1 m away, and at right angles to one another. The height of the nest rim above the ground was measured, the distance from the nearest water estimated, and the drainage of the nest site classed as wet, damp or dry.

Only one visit to a field was made and this precluded any detailed studies on breeding biology. The discovery of duck nests almost always depended on flushing the incubating females, most leaving when the observer was between about 5 to 10 m from them. Bengtson (1970) records that during an Icelandic study 90% of the female ducks were flushed when the observer was about 3 m from the nest. Perhaps up to a third of the ducks nesting at the Washes were missed, so the nesting densities of Mallard and Shoveler *Anas clypeata* presented must be regarded as minimal. The rather open nests of Coot and Moorhen were easily seen and almost all were probably recorded.

Weekly observations of females with broods and of other adults were made from the boundary banks from May to July along the middle third of the Washes. The sizes of ducklings were assessed as being 1/4 or less, <1/2, <3/4 and <4/4 of the size of the parent. These classes have been assigned approximate ages (in days) from the data given on fledging periods in Cramp & Simmons (1977). The brood sizes of Moorhen and Coot could not be properly determined because of their habit of splitting a brood between two parents. Each Moorhen and Coot seen with young was counted as a 'brood'. The habitats used by feeding birds were noted as rivers, ditches, permanent and temporary pools. The latter included some damp areas left as the pools dried out.

Some idea of types and amounts of foods available was obtained by sampling ditches and permanent pools with a 0·25 m diameter pond net of 0·5 mm gauge. Each sample consisted of 10 × 1 m sweeps of the net of a depth of about 0·2 m. In the ditches the net was drawn along the interface between emergent plants and open water. There were less emergents in the pools and the net sometimes scraped the bottom mud.

The feeding methods of adults (except females with broods) were recorded at the permanent pools from May to July. They were classified into: grubbing—where bill pokes below soil surface; grazing—plucking of leaves with the bill; surface picking—the taking of single food items; dibbling—bill under water, head under water, head and neck under water and upending—where bird tips over and submerges the front half of its body. The depth of water in the pools varied from 0 to 0·3 m but was up to about 0·5 m in a few spots (over old ditches). Observations were mainly done in late afternoon or evenings on 40 occasions. As far as possible only 1 record per individual bird was taken on each occasion.

Breeding populations

History

Little seems to be known about the populations of breeding water fowl before the present century. Lack (1934) records that Mallard, Shoveler, Coot and Moorhen bred on the Washes. Table 1 summarizes the recent history. Garganey *Anas querquedula*, Pintail *Anas acuta* and Gadwall *Anas strepera* had become established by the early 1950's and Shelduck *Tadorna tadorna*, Teal *Anas crecca*, Tufted Duck *Aythya fuligula* and Pochard *Aythya ferina* by the early 1960's. Black-tailed Godwit *Limosa limosa* were first recorded breeding in 1952, Ruff *Philomachus pugnax* in 1963, Black Tern *Chlidonias niger* in 1967 (Cottier & Lea 1969) and Little Gull *Larus minutus* in 1975 (Carson *et al.* 1977). Most of these waterbirds have shown general increases at the Washes since their first recorded breeding.

Factors which have changed in favour of breeding birds on the Washes since about 1940, have been: less disturbance from fewer agricultural workers; more nesting cover (and less nest destruction?) which may have resulted from a reduced number of grazing animals; a local increase in damp areas and small pools due to the less rigorous drainage needed to provide for grazing land in the spring.

These small wet areas may have been instrumental in delaying the departures of some of the wintering and passage waterfowl and inducing them to stay and breed. The accelerated increases in the numbers of breeding Tufted Duck and Gadwall is almost certainly related to the areas of permanent water created and maintained by conservation bodies throughout the 1970's. Henny & Holgersen (1974) showed that increases in Gadwall in North America were related to such impoundments.

Effects of flooding 1970–1972

In April, some species, eg. Pintail, are probably remnants of the wintering population, whilst others, eg. Shoveler, had recently arrived. In April 1970 there were about 2·2 times the Mallard, 3·6 times the Coot and 6·5 times the Pintail than in the April 1971 and 1972 whereas the numbers of other species were roughly the same (Table 2). Pintail breeding populations respond favourably to the presence of temporary and seasonal water areas (Krapu 1974).

As the extensive floodwater disappeared in 1970 so did some of the breeding birds. The 150 Pintail pairs gradually dwindled to 34. A similar trend is seen in 1971 and 1972 when there was less water available. Coot gathered into flocks of failed and perhaps non-breeding birds before dispersing. Table 2 also shows that there were at least 55 pairs of waterfowl/100 ha each year. Mallard was the commonest species in 1970 and Moorhen in the two drier springs, when Mallard, Garganey, Pintail and Coot densities were lower. Teal, Shoveler, Tufted Duck and probably Gadwall were

Table 1. May breeding populations (in prs) 1968–1978 and historical notes (mainly after Cambridge Bird Club reports).

Year	68	69	70	71	72	73	74	75	76	77	78	Mean annual density/100 ha
Shelduck	1	1	1	1	1	5	10	12	2	10	6	0·2
Mallard	?	?	1,000	500	400	420	990	1,300	400	880	850	32·9
Shoveler	100+	100+	200	150	200	120	133	306	110	190	217	7·7
Garganey	23	24	12+	6+	7	0	5	9	0	4	6	0·4
Teal	10+	12+	14	14	12	6	20	13	12	12	8	0·5
Pintail	2+	20+	34	2	6	6	3	5	1	5	6	0·4
Gadwall	8	18	12+	18	24	15+	52	40	45	38	51	1·3
Tufted Duck	10	12+	30	30	34	20+	25	50	36	43	50	1·4
Pochard	1	1	2	1	1	1	1	3	0	3	4	0·1
Coot	150	?	416	450	200	50	300	130	50	125	216	9·2
Moorhen	100+	200+	209	600+	150	120	140	150	120	135	?	8·5
Flood into April/May	M	M	M	A			A	M		M	M	62·6

History. Shelduck: 1st recorded breeding 1958. Mallard: 300–800 prs in 1950s. Shoveler: colonized c. 1900; 20–50 prs in 1950s. Garganey: Prob. bred 1942; 5–25 prs in 1950s; 10–15 prs early 1960s. Teal: 1st recorded breeding 1961. Pintail: poss. 1st bred 1927; def. 1951; 4–24 prs 1950s and early 1960s. Gadwall: prob. 1st bred 1951; def. 1953; 1–2 prs to 1967. Tufted Duck: 1st bred 1964. Pochard: 1st bred 1966.

Table 2. Breeding populations of waterfowl (in prs) at times of much (1970) and little (1971 and 1972) flooding in spring.

Species	1970 April Census	1970 May Census	1970 pr/100 ha	av. 1971 and 1972 April Census	av. 1971 and 1972 May Census	av. 1971 and 1972 pr/100 ha
Mallard	1,000	470*	20·7	450	300*	13·2
Teal	9	14	0·6	23	13	0·6
Garganey	6	12+	0·5	10	7	0·3
Gadwall	12	12+	0·5	26	21	0·9
Pintail	150	34	1·5	23	4	0·2
Shoveler	200	70*	3·1	175	75*	3·3
Tufted Duck	44	30	1·3	55	32	1·4
Pochard	6	2	0·1	2	1	0·0
Moorhen	180	209*	9·2	108	440*	19·3
Coot	850	416	18·3	325	356*	15·6
Totals	2,457	1,269	55·8	1,197	1,249	54·8

* Calculated from nesting densities in samples of different habitats searched (Table 3). Values for Mallard and Shoveler must be minima.

fairly similar under both conditions. Tufted Duck and Gadwall nested later than the other species and their populations may have been regulated by the smaller areas of permanent water then available.

Measurements at nest sites

Nests in relation to water

The number of nests found in 1970, the average for 1971 and 1972 and the density of each species in the 5 main habitats are shown in Table 3. In 1970 the high water level meant greater nesting densities of dabbling ducks *Anas spp.* on boundary or ditch banks. Except for Mallard such nest sites were unimportant in the drier years. Wheeler & Harris (1970) also found banks to be important to nesting Mallard in California. The small osier beds seem to be important to Mallard and Moorhen at all times. The favoured sites of Coot and Moorhen were ditches, with higher densities on their banks during wet years. Mallard and Shoveler built their nests on the higher parts of the fields above the Spring flood line (Figure 2, a, b, c). Although most of the flooded land subsequently dried out it remained little used by ducks. In 1970 most of the Moorhen nests built in fields were at the edge or just on the landward side of the flood line whilst most of the Coot nests were within it (Figure 2d). In 1971 and 1972 the nests of both species were more evenly distributed with the greatest densities of the Coot nests in the ditches (Figure 2e). Newton & Campbell (1975) also found that, where habitat permitted, the nests of ducks at Loch Leven were regularly spaced out. Table 4 confirms that most of the duck nests were built on dry ground. Coot nests were usually surrounded by water whilst the drainage at Moorhen nests was variable.

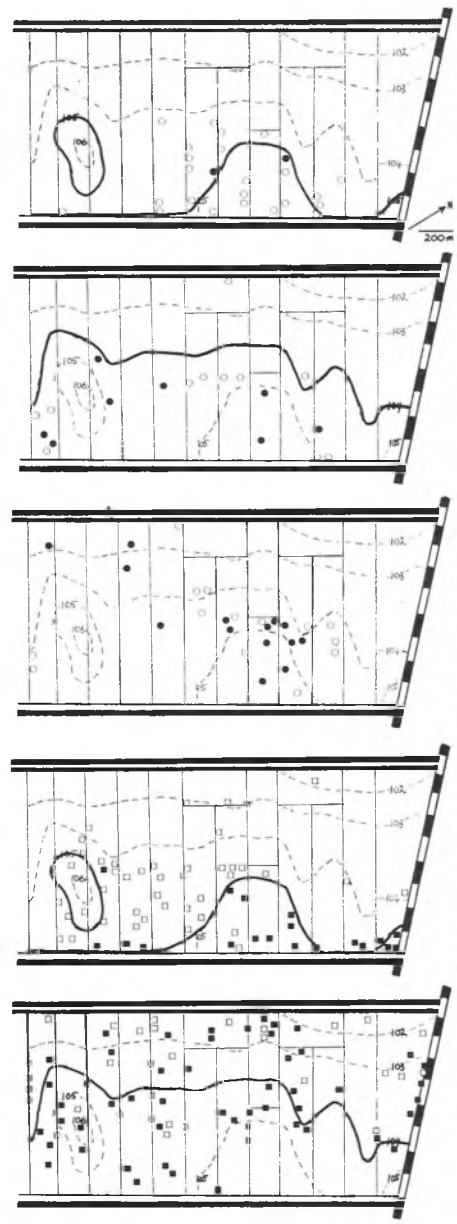

Figure 2. Nest positions in a study area. Mallard ○; Shoveler ●; Moorhen ■; Coot □. Thick line marks flood limit.

Table 4. Water situation at nest sites.

Species	n.	% nests Dry	Damp	Wet
Mallard	240	83	12	5
Teal	3	(100)		
Garganey	1		(100)	
Gadwall	4	(75)	(25)	
Pintail	6	100		
Shoveler	61	75	23	2
Tufted Duck	8	50	38	13
Moorhen	264	21	37	42
Coot	277	8	15	77

The mean distances of nests from water were extremely variable (Table 5), dabbling ducks being between 10–60 m from water. Information from BTO nest record cards (Table 6) for other parts of Britain indicate that Gadwall, Tufted Duck and

Table 3. Nesting densities of waterfowl (prs/100 ha) in different habitats.

Habitat			Boundary banks		Ditch banks		Ditches		Fields		Osier beds	
Year	70	71/72 Av.	70	71/72	70	71/72	70	71/72	70	71/72	70	71/72
Amount available (ha)			261		162		21		1,732		20	
Amount sampled (ha)			53	44	31		4		501		2	
	Nests found		Nest densities									
Mallard	104	72	40	16	97	32			10	10	150	150
Teal	1	1	2						<1	<1		
Garganey	1	1	2							<1		
Gadwall	0	2								<1		
Pintail	14	1	6		10				2	<1		
Shoveler	18	23	4		16	3			2	4		
Tufted Duck	0	2								<1		
Moorhen	53	110			11	2	150	550	8	17	100	125
Coot	106	89			65	11	100	475	16	13	50	50

Table 5. Mean distances of nests from water.

	n	1970 wet distance (m) + SE	n	1971/1972 dry distance (m) + SE
Mallard	103	17·8 ± 15·7	137	29·7 ± 31·0
Teal	1	20	2	90 ± 14·1
Garganey	1	20	1	20
Gadwall	1	10	3	10 ± 2·0
Pintail	14	27·5 ± 22·5	1	70
Shoveler	18	22·1 ± 13·7	44	32·8 ± 26·7
Tufted Duck	2	10·5 ± 14·8	7	9·4 ± 8·5
Moorhen	52	7·2 ± 11·9	213	19·4 ± 23·5
Coot	106	4·0 ± 12·4	169	7·5 ± 19·1

Pochard usually nest within about 10 m of water. Seven of the Teal records refer to nests ranging up to 400 m from water.

Distances from water tended to be less in 1970 than in the two drier years (Table 5). There were significant differences for Mallard ($t_{238} = 3{\cdot}88$, $p < 0{\cdot}001$); Shoveler ($t_{60} = 2{\cdot}07$, $p < 0{\cdot}05$); and Moorhen ($t_{263} = 5{\cdot}30$, $p < 0{\cdot}001$). Coot showed no difference ($t_{273} = 1{\cdot}84$, N.S.).

In 1970 there was no significant difference in the mean distances of nests from water for any comparisons between Mallard, Pintail and Shoveler, nor between Moorhen and Coot. Examining the six species with sufficient samples in 1971 and 1972, there remains no difference between Mallard and Shoveler but there is a difference between Moorhen and Coot ($t_{380} = 7{\cdot}33$, $p < 0{\cdot}001$). There are differences between all the other species pairs except for Tufted Duck/Gadwall, Gadwall/Coot and Coot/Tufted Duck.

Table 6. Distance of nests (m) from water (BTO nest record cards).

	Distance from water (m)				
	0	1–10	11–20	21–100	>100
Pochard	27	3			
Tufted Duck	17	5	1		
Gadwall	3	1			
Garganey		1			
Shoveler	3	5	1	6	
Teal	2	3	3	7	7

Nests in relation to vegetation

Of 78 Coot nests and 86 Moorhen nests, 88% and 80% respectively were without any aerial cover. Of 25 Shoveler nests and 52 Mallard nests, 80% and 65% possessed some cover, with the majority of nests for both species being concealed by a quarter to a half cover. Three Gadwall nests possessed 100% cover.

The dominant plants recorded at the

nest sites are given in Table 7. Those at duck nests were the tussock forming species, mainly tufted hairgrass *Deschampsia caespitosa* and to a lesser extent great pond sedge *Carex riparia* and tufted sedge *Carex acuta*. *Phalaris* and *Glyceria* were much more predominant at Coot and Moorhen nests. The relative importance of these 5 dominant plants are shown in Table 8. The density of Mallard nests in the tussocks is consistently higher than in the non-tussock forming plants. Shoveler seem to favour *Deschampsia* particularly. *Deschampsia* has been found to be favoured by Mallard in Scotland (Newton & Campbell 1975) and California (Wheeler & Harris 1970). Duck nests in *Glyceria* and *Phalaris* were made in tussock-like growths which had probably been produced by selective grazing.

Mallard and Shoveler nests were mostly constructed between two or more adjacent tussocks with some alongside them, or within a large tussock with the vegetation arranged into a cupola over the sitting female. The greatest density of Coot nests was found in *Glyceria* while Moorhen nests were more evenly spread throughout the plant range.

The height of vegetation at the nest was significantly greater than the height around the nests for all species (t tests $p < 0{\cdot}05$ (at least) in all cases) except for Garganey and Teal where the samples were too few (Table 9).

The height of vegetation at the nests was significantly different ($p < 0{\cdot}005$, at least) for all species comparisons in Table 9 except for Mallard/Coot, Pintail/Shoveler, Shoveler/Tufted Duck and Tufted Duck/Moorhen, and for any comparisons involving Garganey and Teal (samples too small).

The height of the nests within the vegetation was greatest in those species that nested closest to water, especially Coot and Moorhen, thus minimizing adverse effects of rising water levels.

Nests in relation to field management

In Table 10 the density of nests found is related to the *previous* year's field management. The greatest density of Shoveler nests were found in areas that were grazed in excess of 90 cow days/acre (222/ha) and in hayfields that were subsequently grazed.

Table 7. Dominant plants at nest sites in 1970 and average of 1971 and 1972.

	*% nests									
	Mallard		Shoveler		Other Ducks		Moorhen		Coot	
	1970	71/72	70	71/72	70	71/72	70	71/72	70	71/72
Plants (number)	103	68	18	22	11	9	53	109	108	87
	%	%	%	%	%	%	%	%	%	%
Deschampsia caespitosa	47	16	61	58	55	12	11	6	1	
Urtica dioica	17	11					2			
Agropyron repens	17	7	11							
Phalaris arundinacea	19	31	28	35	36	53	34	33	35	31
Glyceria maxima	18	11	17	12		12	47	47	61	59
Carex acuta	15	4	11				2	6	4	6
Carex riparia	7	26	17	12		12	13	8	3	6
Rumex crispus	7	1	11				13	10	19	8
Carex disticha	2		6	7			4	3	1	
Other spp.	17	14	17	2	9	12	15	14	11	9

* % do not add up to 100 because some plants were co-dominant.

Table 8. Density of nests (per 100 ha) in tussock and non-tussock forming plants.

Area (ha) plant sward sampled		Mallard		Shoveler		Moorhen		Coot	
		70	71/72	70	71/72	70	71/72	70	71/72
Tussock forming									
Deschampsia caespitosa	56	86	20	20	23	11	13	2	0
Carex riparia	60	12	30	5	5	12	15	5	7
Carex acuta	30	50	10	7	0	3	20	13	7
Non-tussock forming									
Glyceria maxima	240	8	3	1	1	10	21	28	21
Phalaris arundinacea	300	6	7	2	3	6	12	13	9

Mallard favoured unused fields or lightly grazed fields. Taking the pastures only, the difference between the two species is significant (α^2 27·5 $p < 0{\cdot}001$). The smaller samples for the other duck suggest that Gadwall and perhaps Tufted Duck prefer unused or lightly grazed fields and that Pintail prefer fields that have been more heavily grazed in the previous year. The siting of Coot and Moorhen nests does not seem dependent on any form of management. The small area of osier wood sampled yielded high densities of Moorhen, Coot and Mallard nests.

Page & Cassel (1971) found five times as many ducks nesting in unhayed areas than hayed ones in N. Dakota. Under experimental conditions there Oetting & Cassel (1971) found that significantly more Mallard, Pintail and Gadwall chose to nest in unmown rather than mown fields; there was no difference with Shoveler. Martz (1967) found, also in N. Dakota, that Gadwall nested readily along unmown shorelines, Pintail and Shoveler in mown meadows.

Habitats of adults and broods

Feeding areas

Figure 3 shows the habitats utilized by female ducks and adult Moorhen and Coot with broods. All 10 Shelduck broods were seen in rivers as were 31% of the Tufted Duck broods. Ditches contained the largest numbers of Moorhen, Coot, Shoveler and Mallard broods, whilst permanent pools held most of the Gadwall and Teal. Temporary pools contained fewer broods of any species except possibly Mallard and these were mostly early in the season.

Figure 3 also shows that rivers and ditches were seldom used by adult birds without young, except for Tufted Ducks and the small number of Pochard seen. Gadwall favoured permanent pools, Coot, Mallard and Pintail temporary pools. About equal numbers of Shoveler, Teal and Garganey were found in the two pool types.

In the case of Coot and Mallard (Figure

Table 9. Mean height (cm) of vegetation at, around nests, and of nest rim (±SE).

Species	Sample	At nest	Around nest	Nest rim
Pintail	6	26·0 ± 7·0	11·0 ± 4·0	10·0 ± 5·0
Garganey	1	28·0	16·0	5·0
Shoveler	61	28·8 ± 8·7	16·3 ± 9·8	6·8 ± 3·7
Tufted Duck	9	32·9 ± 7·6	29·9 ± 7·0	8·7 ± 3·0
Teal	2	35·0	25·0	4·0
Moorhen	264	37·4 ± 14·9	25·1 ± 16·8	14·2 ± 7·4
Mallard	238	40·0 ± 13·9	27·6 ± 15·4	9·0 ± 5·2
Coot	283	41·0 ± 15·3	32·8 ± 16·7	18·0 ± 8·4
Gadwall	4	57·5 ± 5·0	40·5 ± 7·9	10·3 ± 5·6

Table 10. Density of nests (per 100 ha) in relation to the field management of the previous year. Grazing measured in cow days/acre (cd/a).

Habitat	Woods		Pastures								Hayfields			
Grazing (cd/a)	0	0	1–30	31–60	61–90	91–120	121–150	151–180	181–210	210–240	0	1–30	31–60	60–90
Area (ha) searched	5	88	84	200	154	232	54	145	20	7	75	75	103	47
Mallard	200·0	18·2	34·5	12·5	16·2	13·4	11·1	13·1	10·0		20·0	12·0	14·6	8·5
Teal								0·7						
Garganey						0·4							1·0	
Gadwall		1·2		0·5	0·7									
Pintail				0·5		1·7		2·1						
Shoveler			2·4	1·0	3·3	6·5	7·4	6·9	45·0	14·3	1·3	5·3	4·9	4·3
Tufted Duck			1·2		0·7			0·7						
Moorhen	140·0	6·8	17·8	14·5	14·9	25·0	13·0	17·2	15·0		9·3	21·3	19·4	8·5
Coot	40·0	13·6	16·7	26·5	14·9	24·6	5·6	11·7	20·0	28·6	5·3	17·3	23·3	

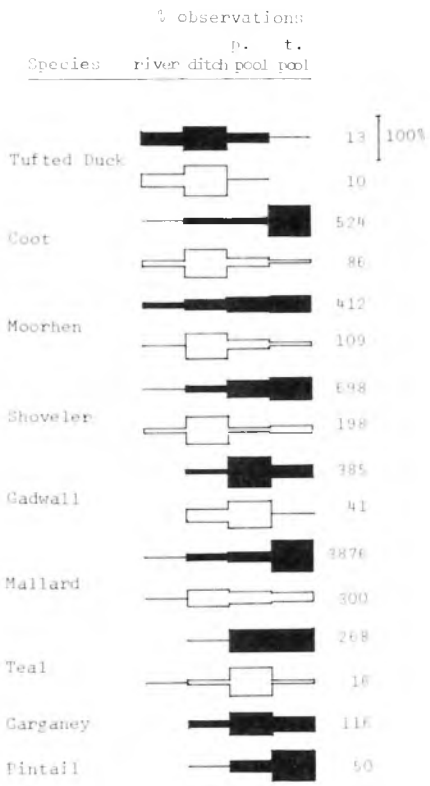

Figure 3. Habitats used by females with broods (□), and other adults (■).

3) there was a clear intra-specific separation with broods using ditches and other adults feeding in temporary pools. Broods of Moorhen and Shoveler fed in ditches while other adults fed in permanent and temporary pools. Teal show the same trend. Tufted Duck broods and other adults both fed on rivers and ditches but were always apart. The same was true of Gadwall on the permanent pools. Here, females with broods seemed to keep nearer the edge of the pool.

These strategies may reduce competition for food or allow more peaceful feeding by reducing the chance of intra-specific aggression between the mother and other adults. Such disturbances usually scatter broods and could result in losses, especially by predation. Escape cover and shelter is close at hand in ditches, and they tend to be richer in the number and variety of invertebrates which may also be more accessible in the sheltered water and amongst the plants than they would be in open pools.

After ducklings and young Coot reached about three-quarters of adult size they began to associate with feeding groups of adults. Well grown Moorhen dispersed but some were seen acting as 'nurses' to younger birds.

It was suspected that Moorhen and Coot broods were kept within a fairly static home range but that some of the duck broods were more mobile. Shelduck broods may be moved into the New Bedford River and led towards the coast, one brood being almost certainly taken 8 km within about 12 hours of hatching. Shelduck has only recently become an inland nesting bird and may not yet have adapted to rearing broods in freshwater habitats.

Food abundance and availability

The commonest emergent plant in ditches was *Glyceria maxima*, sometimes branched burreed *Sparganium erectum*. The commonest submergents were rigid hornwort *Ceratophyllum demersum*, small pondweed *Potamogeton berchtoldii*, water starworts *Callitriche spp*; common duckweed *Lemna minor* was always present in variable amounts on the water surface. *Glyceria* was also the main emergent in the pools with smaller amounts of amphibious bistort *Polygonum amphibium* and common spike rush *Eleocharis palustris*. There were isolated patches of *Potamogeton berchtoldii* and the algae *Spirogyra sp.* and *Cladophora sp.* and large amounts of bare mud (detritus and peat).

Table 11 shows the potential foods in mid-June for 10 ditch and 4 pool sites. Hirudinea, Turbellaria and Arachnida were found in small numbers as were annelids except for *Lumbriculus variegatus* which was found in great numbers in the pool mud. Planktonic crustaceans, especially Ostracoda, were abundant in the pools. Other common species were *Daphnia longispina, Simocephalus expinosa* and *Chydorus sphaericus*. Up to 3 species of cyclopoid copepods were common, especially in the pools. Most of the remaining crustaceans were the relatively large *Gammarus pulex* and *Asellus aquaticus*.

Easily the most abundant insects were Chironomidae larvae and pupae. *Chironomus sp.* were present just below the surface of the mud and *Tanypus sp.* at or above the mud surface. The adult flies were very abundant on the emergent plants but few were caught in the pond net. Small-numbers of Culicidae larvae and pupae were also found.

Table 11. Potential foods in samples taken in ditches and permanent pools in June.

Taxa.	No. of spp	Ditches (n = 10) No. of individuals av.	range	Permanent pools (n = 4) No. of individuals av.	range
Turbellaria	3	1	0–5	1	0–3
Annelida	2	22	0–120	558	6–1,000
Hirudinea	7	8	0–23	5	0–12
Arachnida	2+	40	1–155	1	0–3
Nematoda	?	+		+	
Crustacea					
Cladocera	4+	1,695	20–9,000	118	28–180
Copepoda	3+	825	100–3,000	2,200	1,000–4,000
Ostracoda	1+	2,660	100–5,000	10,750	4,000–14,000
Others	3	76	1–200	223	1–750
Insecta					
Chironomidae (1 + p)	2	865	116–3,040	803	231–2,160
Others	15	177	2–1,300	30	2–70
Mollusca	20	169	7–532	21	1–43
Pisces	2	1	0–4	0	

Gastropod molluscs were much commoner in the ditches than in the pools and this is associated with the greater amounts of plants. The commonest species were *Bithynia leachi, Planorbis leucostoma* and *P. vortex*. In some unsampled ditches *Potamopyrgus jenkinsi* was extremely abundant on the mud surface.

Duckling feeding

The main feeding methods observed were pecking at objects at or just under the water or off plants. Ducklings sometimes snapped at objects near them in the air. Older ducklings sometimes fed with their heads and necks under water whilst young Tufted Ducks dived. Coot and Moorhen chicks were sometimes fed by their parents with what appeared to be bits of filamentous green algae or pond weeds *Potamogeton spp.*

However, it was clear that most ducklings fed near the surface of the water and the main foods must have included the larger planktonic Crustacea, and all the life stages of Chironomidae. Gastropod molluscs may have been important to birds feeding in shallow water or amongst emergent plants. At other times of the summer other invertebrates were more plentiful and would have almost certainly been eaten, eg. the hemipteran bugs *Sigaria dorsalis* and *Callicorixa praeusta* and the adults and larvae of the beetles, *Hydroporus, Hygrotus* and *Haliplus spp*. These findings accord to the findings of Bengtson (1971, 1975) in Iceland, and Lees & Street (1975) and Street (1977) in Buckinghamshire. They found that adult chironomids and beetles were taken by young dabbling ducks, and chironomid pupae, planktonic Crustacea, and molluscs by young diving ducks.

There was a degree of temporal separation between the broods of some species which would allow for the partitioning of food resources. About a half of the Mallard broods were encountered in May, and about a half of the Shoveler broods in the first half of June. Gadwall, Teal and Tufted Duck broods were all seen throughout June and July.

Adult feeding

The methods used are shown in Figure 4. Coot largely grazed the leaf tips, mostly of *Glyceria maxima, Polygonum amphibium* and *Eleocharis palustris*. Just over a half of the grazing records were by birds walking in very shallow water. Of the feeding records 29% involved bringing submerged plants, *Spirogyra sp., Cladophora sp.* and *Polygonum berchtoldii* from a depth of up to about 18 cm to the surface where they were sorted. Pieces of vegetation were ingested and sometimes smaller items, possibly invertebrates quickly picked out. Moorhens mainly walked in shallow water and picked small animals off plants, the

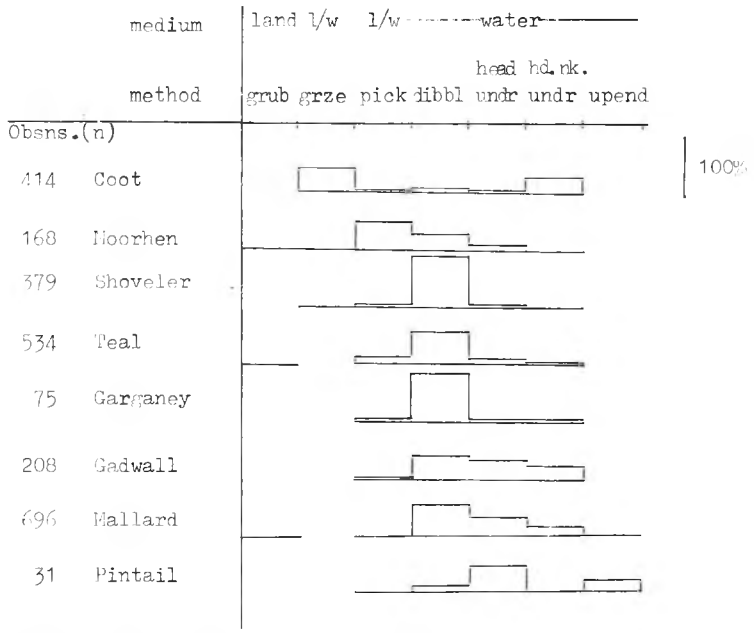

Figure 4. Feeding methods of adult waterfowl in summer.

surface of the water or to about 3 cm below the surface. Many of these actions involved a forceful stab just below the surface. Some of the items picked off the water were almost certainly pieces of vegetation brought up and discarded by Coot.

Shoveler, Teal and Garganey mainly fed by dibbling, the latter two in the top 4–5 cm of water, Shoveler down to 7 cm. Shoveler fed swimming in more open water than the other two species. The commonest position was with the bill held in the water at an angle of about 45° to the vertical. Sometimes the bill was held almost horizontally near the water surface. The main foods taken must have included the larvae and pupae of Chironomidae and the abundant planktonic Crustacea. Feeding with the bill in the horizontal position may have been a device used when the prey were near the surface. Samples taken from areas where Shoveler had fed whilst swimming in tight full and half circles showed that large quantities of Ostracoda were present in the water.

Almost all the Garganey fed whilst swimming but about a half of the Teal were walking in shallow water. One or two Garganey were the most seen at any one time and they kept to more open water than did the small parties (usually 6–10) of Teal. Teal were more mobile feeders than Garganey but were less so than Shoveler. They probably took similar foods to the Shoveler but perhaps not so much of the smaller animal plankton which could be more easily sieved out by the latter's longer and closer-spaced bill lamellae.

The three larger *Anas spp.* fed more with their heads or heads and necks submerged in deeper water. Gadwall fed between about 5 and 23 cm below the surface, especially over growths of submerged plants. Filamentous green algae and *Potamogeton spp.* were probably the main foods, but the taking of some invertebrates would have been unavoidable. Most ingestion took place with the head under water but occasionally filamentous plant growth was seen in the bill of a feeding bird. Presumably this diet accounted for the fact that Gadwall were the least mobile of all feeding ducks.

Mallard fed between about 6 to 28 cm below the surface of the water and were fairly mobile, regularly changing their feeding positions by 15 cm or so. They fed in both open water and amongst emergents. Pintail at times use deeper water (11–41 cm) than Mallard. Both species would have the full range of benthic invertebrates at their disposal including the larvae and pupae of Chironomidae spp. and the abundant worm *Lumbriculus variegatus*, the latter being probably out of reach of some of the other ducks. Birds

feeding amongst emergents would also have access to a range of molluscs.

Productivity

Deserted nests

Of 240 Mallard nests 23% were deserted, as were 19% of 58 Shoveler, 15% of 260 Moorhen and 17% of 275 Coot nests. All but one of the deserted Mallard and all the Shoveler nests had probably been predated by Carrion Crows *Corvus corone* and/or been trampled by cattle. A quarter of the deserted Moorhen nests and almost half the Coot nests had been flooded, the remainder having been predated. There does not seem to be any relationship between predation and the degree of cover over the nests of any species. De Jong (1977) in the Netherlands records that cattle at densities of 400 per ha during the breeding season caused losses of over a half of the meadow bird nests by trampling or disturbance.

Clutch and brood size

The clutch sizes in Table 12 are based on unpredated nests where there were 5 or more eggs when found. There were no detectable annual differences for species over the three years. The results for Mallard, Shoveler and Tufted Duck are about 1 egg less than Hildén (1964) found in Finland.

There was a great number of records of Mallard broods up to about 10 days old but many fewer with the older age classes (Table 13). This 64% drop between the first two age classes is similar to that recorded by Street (1977) in Buckinghamshire and Ball *et al.* (1975) in Minnesota. Such a drop was not observed with the three other ducks shown in Table 13. The Mallard losses at the Washes coincided with low minimum grass temperatures on several nights in May (between 5 and 8 nights in each May of the study years had a temperature of 1°C or less). Dead Mallard ducklings were commonly seen after such

Table 12. Mean clutch sizes (±SE).

	Mallard	Shoveler	Garganey	Tufted Duck	Moorhen	Coot
n	139	34	2	4	132	127
Mean	7·9 ± 1·7	8·4 ± 1·6	10·5	6·8 ± 1·3	7·4 ± 1·9	6·8 ± 1·5

Table 13. Mean brood size and age classes of waterfowl.

Species	Size of ducklings	n	Brood size Mean ± SE
Mallard	<1/4	211	6·3 ± 3·0
	<1/2	76	4·0 ± 2·6
	<3/4	45	3·2 ± 2·0
	<4/4	14	2·5 ± 2·3
Shoveler	<1/4	40	7·1 ± 3·3
	<1/2	57	5·3 ± 2·5
	<3/4	28	4·4 ± 2·7
	<4/4	30	3·8 ± 2·5
Gadwall	<1/4	12	4·0 ± 2·1
	<1/2	12	5·3 ± 2·5
	<3/4	9	5·7 ± 2·5
	<4/4	5	3·6 ± 2·1
Tufted Duck	<1/4	25	4·5 ± 2·3
	<1/2	15	4·5 ± 2·5
	<3/4	3	3·0 ± 1·0
	<4/4	4	3·3 ± 1·5

Size of ducklings assessed as a fraction of nearby parent. Approximate ages of birds: <1/4 = 1–10 days; <1/2 = 11–20 days; <3/4 = 21–30 days; <4/4 = 31–45 days.

evenings. It was uncertain whether they died from hypothermia or from starvation resulting from a depressed food supply brought about by the inclement weather. Most of the Shoveler and other ducks broods appeared from June onwards and were not subjected to these ground frosts.

The mean brood size of almost fully grown young ranged from $2{\cdot}5 \pm 2{\cdot}3$ for Mallard to $3{\cdot}8 \pm 2{\cdot}5$ for Shoveler. There were no significant differences between the species. The size of the Shoveler broods may not be as accurate as the other species because of creching. Wherever possible allowances were made for this by dividing any large group of young by the number of females seen in attendance. The largest crêche had at least 40 young and seemed the product of at least 6 females.

Predation by Carrion crows, large gulls *Larus spp.* and rats *Rattus norvegicus* may have been responsible for chick losses but very little was actually observed. Duebbert & Kantrud (1974) in S. Dakota found that large scale reduction of predators did not significantly affect duck production in areas where there was good ground cover.

From the clutch sizes in Table 12 and the brood data in Table 13 we can crudely calculate the production of ducklings based on the method of Street (1977).

Mean size of newly hatched brood (assumed to be 95% of clutch size) × [(n broods 4/4 ducklings)/(n broods 1/4 ducklings)] % × [(mean size of 4/4 broods)/(mean size of newly hatched brood)] %.

The production of Mallard is about 0·2/pr, Shoveler 2·9/pr and Tufted Duck 0·5/pr. Assuming the clutch size of 9·96 for Gadwall obtained Balat & Folk (1968) in Czechoslovakia, the production of Gadwall would be 1·5/pr.

Observations of recently fledged birds which had joined up into small flocks were made mostly on the permanent pools and provide another (minimum) estimate of productivity. The totals seen are compared to the calculated productivity (in brackets) where this has been possible to work out. Up to 10 recently fledged Pintail, Pochard, Garganey and Teal were seen annually and up to 20 Tufted Duck (15) and Gadwall (31). Up to 150 recently fledged Shoveler were seen (220) and 100 Mallard (80). However in 1974 Mallard fledged at least 1,000 young when there was suitable water and no frosts in May. Probably about 50 Moorhens and Coot were fledged each year between 1970 and 1972.

Discussion

Two groups of factors affect the ecology of the breeding waterfowl. Firstly, there are the requirements of an adequate, exploitable food supply, dependent on the presence of standing water and damp areas. These factors are 'ultimate' ones and at all times affect the presence of adults and the survival of young. The requirements need to be met for about 150 days, from the time that pre-breeding territories are set up (March) until the broods of late nesting species are fledged (July).

Secondly, there are requirements for suitable sites for nesting, shelter against adverse climate, cover against predators and disturbance-free surroundings. These need to be met in one spot for each female for some 30–50 days between the start of egg-laying and the leading away of the hatched chicks. They are needed for a further 50–60 days, in a variety of locations, whilst a brood is reared.

Prior to incubation both groups of factors are within the home range that pairs adopt. Studies using telemetry in North America have shown that the home ranges of Pintail are about 500 ha, Mallard 200 ha, and Shoveler and Gadwall less than 100 ha. (Poston 1974, Gilmer 1975). For each species there can be a considerable overlapping of home ranges but within them there are much smaller 'core-areas' which are effectively used by only 1 pair of ducks. In the case of Shoveler the core area is only about 0·9 ha (Seymour 1974). Gilmer (1975) has shown that the home ranges of Mallard are smaller in places where the density of non permanent wetlands (less than 0·2 ha) are highest.

No work was done on home ranges at the Washes but there is some relation between population sizes and the amount of water present in the spring.

In 1970 the spring flood covered, at its maximum, just over a half of the Washes and there were 108 pairs of potentially breeding waterfowl per 100 ha. In the other 2 years less than a quarter of the Washes were flooded and there was an average of 49 pairs of potential breeders per 100 ha. These results are similar to the findings of Hunt & Naylor (1955) in California. Furthermore, the fact that these floods disappeared leaving only about 102 ha of wet areas in May (ditches and pools) had a further effect on the 1970 populations. The April populations were reduced by about a half to 56 pairs/100 ha of water-

fowl by May. The reduction of water was less in the other two years and both the April and May populations averaged about 55 pairs/100 ha. These results are similar to those of Stewart & Kantrud (1974) in N. Dakota. They found that populations fluctuated considerably due to yearly variations in frequency, density and area of basin wetlands with surface water. Thus, the benefit of a spring flood on the Washes in holding the breeding waterfowl is lost if the levels are not maintained for the rest of the breeding season. At the Washes the populations most affected were Mallard, Pintail, Coot and probably Garganey. However, Teal, Shoveler, Gadwall and Tufted Duck populations remained fairly static under both sets of spring floods. The fact that they nest later (May onwards) than the other species means that they do so when the water areas are smaller and somewhat stabilized. Tufted Duck and Gadwall may be more dependent on permanent water areas anyway.

In 1970–1972, 2–5% of the Washes remained covered by suitable water areas. De Jong (1977) describes a similar situation for some artificially created damp meadowland in Holland where waterfowl populations vary between 49–165 pairs/100 ha. Here the water present is also a minority of the total habitat. In an opposite situation, where water occupies much larger proportions of habitats, duck densities are much higher. At Lake Myvatn, Iceland (Bengtson 1970) the nesting densities of ducks reach 600 pairs/100 ha and up to 850 pairs/100 ha on islands. Newton & Campbell (1975) showed that density of duck nests on a 42 ha island on Loch Leven in Scotland is about 2,380 pairs/100 ha. The main reason for these higher densities is that the greater water areas allow more pairs to set up pre-breeding territories and to retain suitable feeding areas for the remainder of the breeding cycle. The conclusion is that, at the Washes, suitable feeding areas are at a premium, especially from May onwards and that there is an excess of suitable nesting habitat relative to the amount of suitable feeding areas. Hence, the relatively low densities of breeding waterfowl.

The main foods used by waterfowl and their young probably include Chironomidae (all life stages), planktonic Crustacea and molluscs. The first-named are possibly the most important. At the Washes chironomids are commonly found in the ditches and pools. Their distribution and availability as foods is almost certainly curtailed as the seasonal pools dry up. Ditches and permanent pools are mostly used for feeding by waterfowl broods and initially, at least, the temporary pools are used mainly by adults not connected with any broods. The temporary pools are probably homologous with the areas that receive the 'spring run offs' in North America (Swanson *et al.* 1974). When the dead vegetation of the previous year is inundated a 'hay infusion' situation develops. Primary consumers quickly become abundant and include filter feeders such as cladocerans and mosquitos and grazers such as molluscs. Secondary consumers include beetle and dragonfly larvae. Overall, a high standing crop of invertebrates develops and is exploited by feeding ducks. At the end of the summer these areas are dry.

Bengtson (1972) has associated a relative scarcity of chironomid larvae with high rates of nest desertion and reduced production. Newton & Campbell (1975) ascribe the shortage of suitable brood rearing areas as the major factor for the low production of dabbling ducks at Loch Leven. As the summer progresses the latter situation may also be true at the Washes. Predation does not seem to be a major factor causing duckling loss. In his study Bengtson (1972) estimates that only about a quarter of duckling losses are due to predation.

Water is also involved in determining some of the physical characters required by breeding waterfowl. Hoffman (1970) shows a relationship between the number of territorial pairs of ducks and the length of shoreline (probably part of a 'core area') that males are able to defend. At the Washes the temporary flooded areas give additional opportunities to those provided by the shorelines of permanent pools and ditches.

Choosing a nest site may also involve two other features which were not studied. Firstly, there may be some innate or learned judgement made by a nesting bird concerning the habitat. Klomp (1953) has shown that Lapwings *Vanellus vanellus* are able to judge the final quality of the nesting habitat from some early season features. Secondly, as Bengtson (1970) points out, experience probably influences habitat selection in ducks. They have a strong site tenacity and tend to return to nearby areas each year. This may be particularly the case with successful females or their progeny.

The 9 species of breeding ducks on the Washes represents a range that is comparable to most other studies. However, only Mallard and Shoveler can be regarded as common. The remaining species nest at low densities and in certain years (Table 1) some may be rare or absent. This emphasizes the point that conditions on the Washes are marginal, especially for Garganey and Pintail. A slight permanent change in the water regime involving less water being present in the spring could well see their disappearance as regular breeding species. This has already happened as a result of the improved drainage on the nearby Nene Washes. However, in a year of exceptional spring flooding as in 1979, the Nene Washes can still be attractive to breeding ducks (C. J. Cadbury and P. Round, pers. com.). Based on counts of males in May they calculate that Pintail and Garganey each nested at a density of 0·3 pr/100 ha with Shoveler at 8·9 and Mallard at 46 prs/100 ha, comparable to averages for the Ouse Washes (Table 1).

Round (pers. com.) has also found the densities of ducks to be low in other flood plain areas where drainage has been improved. In the Yare Basin, Norfolk, he calculates that Mallard nest at a density of 4·1 pr/100 ha, Shoveler at 0·3 pr/100 ha with no Pintail and Garganey. The Somerset Levels have virtually lost their breeding complement of wildfowl except for Mallard which breed at an overall density of only 2·1 prs/100 ha. Gravel pits alongside the River Ouse about 80 km up stream of the Ouse Washes support breeding Mallard at a density of about 11·3 prs/100 ha and Tufted Duck at 9·0 prs/100 ha (M. Street, pers. com.). Interestingly the density of Mallard and Tufted Duck nesting on the disturbed open pools and lakes are 4·9 and 4·2 prs/100 ha respectively, whilst inside the reserve there, in the undisturbed sheltered feeding areas, densities reach 58·3 and 44·4 prs·100 ha respectively.

Niche differences

Hildén (1964) found that there was some differences in the choice of nest sites and in habitat preferences of ducks but little ecological segregation. The main differences probably lay in their feeding habits.

Weller (1972) showed that there was little competition amongst 11 breeding species of waterfowl in the Falkland Islands because there was a diversity of 'habitat niches' which provided different sources of food. Where two species used the same 'habitat niche' they tended to differ in the trophic (= food) niche although the situation with the *Anas spp.* was more complex. There may have been overlaps in the food taken.

We have seen that there are fewer differences in distances of nest from water amongst 6 species of waterfowl at times when the Washes are flooded. In the two years when they were unflooded 11 of the 15 pairs of species combinations were significantly different from one another (Table 5) but the range for each species was high. Ducks selected nests amonst tussock forming plants whilst Moorhen and Coot did not. There were also some species differences in the height of vegetation at nest sites. Of the 21 pairs of species comparisons in Table 9 there were significant differences between 17 of them, although the differences between the nearest neighbours was not always so. Again, there was a great variation in the height of vegetation at the nests of most species. Shoveler chose to nest mostly in areas grazed in excess of 90 cow days/acre (222/ha) in the previous year, whilst Mallard nested in areas grazed below this density. There was no difference between Moorhen and Coot. The competition for nest space is probably not great at the Washes in most years.

Teal and Gadwall broods were mostly found in permanent pools. Shoveler, Tufted Duck, Moorhen and Coot broods were mostly found in ditches with rivers as an important secondary habitat for Tufted Duck. Mallard broods seemed to have the greatest niche breadth being found in ditches, permanent and temporary pools. This probably accounts for the fact that they were the commonest breeding duck on the Washes.

Figure 5 attempts a partially objective comparison of the niches of adults not involved with broods. Two components are presented: one part, H, representing the habitat used (from data in Figure 3) and the other, M, the zone (including depth) and/or method of feeding based on Figure 4. Of the 36 niche comparisons, 30 (83%) are separated by at least 1 of the factors. Coot, Moorhen, Gadwall and Tufted Duck are separated in all comparisons. The comparison of Mallard/Teal, Shoveler/Garganey, Mallard/Garganey and Mallard/Pintail have both factors overlapping, but the combined differences may be enough for them to be ecologically sepa-

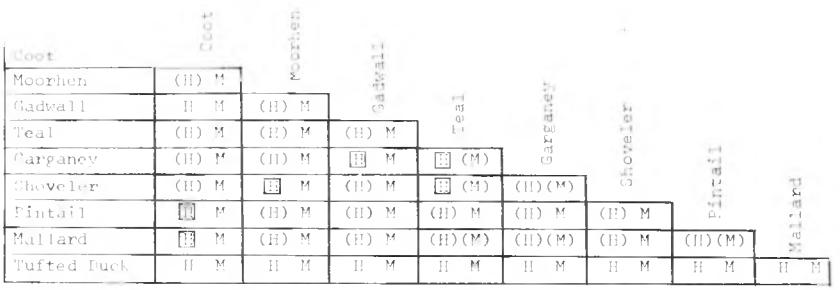

Figure 5. Interspecific comparisons of habitat niches among adult waterfowl during the breeding season. H = habitat, M = zone + method of feeding. No, partial ( ) and complete □ overlap.

rated. Teal/Garganey and Teal/Shoveler were partially separated by virtue of feeding methods. Further and more precise differences may be found if it was known what the different ducks fed on. Also, since most of these overlapping pairs involve Shoveler and Teal there may be some advantage to them if their closely spaced bill lamellae are able to filter out smaller food items. This was at least shown to be functionally possible during winter food studies (Thomas 1978). However, it may be that there is naturally an overlap of niches in spring when invertebrate foods are abundant.

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Summary

Between 1968–1978 the mean annual density of breeding waterfowl at the Ouse Washes has been 63 prs/100 ha. Most species have shown general increases over the last 30 years and coincide with a slightly less rigorous drainage policy in the Spring. Breeding Gadwall *Anas strepera* and Tufted Duck *Aythya fuligula* have greatly increased due to the permanent pools provided in the last 10 years. Pre-breeding populations, especially of Mallard *Anas platyrhynchos*, Pintail *Anas acuta* and Coot *Fulica atra* were markedly higher when there were large amounts of spring floodwater.

Dabbling ducks nested on higher ground, particularly the boundary and ditch banks, in the wetter springs. Their nest sites were on dry ground whilst those of Coot were surrounded by water: Moorhen *Gallinula chloropus* nests were intermediate. Gadwall, Tufted Duck and Pochard *Aythya ferina* nested within 10 m of water whilst other duck species nested between 10–60 m from water. The preferred duck nest sites were in tussocky growths, especially of *Deschampsia caespitosa*, whilst Coot preferred the non-tussocky *Glyceria maxima*. The height of vegetation at the nest was greater than around the nest for all species. Competition for nest space is probably not great in most years.

Mallard and perhaps Gadwall and Tufted Duck preferred to nest in unused or lightly grazed fields whilst Shoveler *Anas clypeata* and perhaps Pintail preferred the more heavily grazed fields (>90 cow days/acre). Coot and Moorhen showed no such preferences. Ditches and permanent pools held most of the waterfowl broods, whilst the temporary pools held most of the adults not involved in rearing young. The main duckling foods were probably the larger planktonic *Crustacea* and all the life stages of *Chironomidae*. The productivity of waterfowl appears low, with the mean brood sizes at fledging ranging from 2·5 for Mallard to 3·8 for Shoveler. At least for Mallard the greatest reduction in brood sizes occurred between quarter and half-grown young and coincided with low minimum grass temperatures in May. Also, suitable feeding areas are at a premium from May onwards as the water-bodies diminish.

Mallard and Shoveler are the commonest ducks, whilst the remaining species nest at low densities and in some years are absent or rare. Consistently less water present in the spring in the future could see the disappearance of such species. In comparison to areas where water is a majority habitat the washes waterfowl populations are low. However, they are greater and richer in species than flood plains which have largely been drained for agriculture.

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Dr G. J. Thomas, RSPB, The Lodge, Sandy, Bedfordshire, SG19 2DL.