The ecology and mortality of swans at the Ouse Washes, England

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Introduction

As is pointed out in a subsequent paper (Cadbury, 1975) the Ouse Washes hold a large proportion of the western population of the Bewick's Swan *Cygnus columbianus bewickii* in winter, as well as many Mute Swans *C. olor* and Whooper Swans *C. cygnus.* This paper describes the food and feeding ecology of these swans and examines the causes of winter mortality.

The analysis of gut contents is the traditional method of assessing the food of wildfowl, but as swans have long been protected there has been little opportunity for examining their diet by this method. The food of swans has recently been reviewed by Owen & Kear (1972). There is little published information on the food of Bewick's Swans apart from a study of feeding in brackish water in the Netherlands (Brouwer & Tinbergen, 1939). Here the swans fed on the leaves and rhizomes of aquatic plants, mainly pondweeds *Potamogeton* spp. Similarly eight stomachs examined in Denmark contained only *Potamogeton* and eelgrass *Zostera* rhizomes and roots (Sparck, 1957). There is, however, little information about the food on flooded grassland which has been the main habitat of the Bewick's Swan in western Europe in recent winters, though some have taken to feeding on agricultural land (Merne, 1972).

The food of Mute Swans on freshwater habitats in Britain has not been studied, although much is known about their use of tidal areas (Gillham, 1956; Berglund *et al.* 1963; Mathiasson, 1973). Here they feed on *Zostera, Potamogeton* spp., stoneworts, *Chara* spp. and green algae.

Accidents are responsible for a large proportion of swan deaths in winter. Collisions accounted for half of British Mute Swan deaths (Ogilvie, 1967), and other human activities were responsible for another 30%. Human agencies are also responsible for most of the reported deaths of other species (Beer & Ogilvie, 1972). Data are presented here on the causes of death of swans found on the Ouse Washes between 1968–1969 and 1974–1975.

Materials and methods

As the corpses of swans are conspicuous and are not easily removed by scavengers, most of those which died at the Ouse Washes over the winters 1969–1975 were probably located in the course of regular visits. Where possible the whole body was collected, deep frozen and subjected to a full post-mortem examination including X-raying. The causes of death of 35 swans were so ascertained during the study. Where it was impossible to preserve the intact bird, the gut was stored in 5–10% formaldehyde; those of 20 Bewick's, 2 Whooper and 8 Mute Swans were examined.

A complete post-mortem examination was carried out whether or not the cause of death was already known. Swans involved in collisions were characterized by severe bruising and sometimes singeing if they had struck power lines, while radiographs of shot birds showed lead pellets embedded in tissues. Birds which had died of lead poisoning were emaciated, and had vivid green gut and gizzard linings. Eroded pieces of lead were then generally present in the gizzard, and occasionally these could be seen on a radiograph.

Material from the oesophagus was sorted, dried and weighed. Vegetation from the gizzard was only analysed if there was very little in the oesophagus or if its contents appeared different. Seeds and vegetative material were treated separately as they probably passed through the gut at different rates. Grit was dried, weighed and sieved through meshes of 2 mm, 1 mm and 0·5 mm to ascertain its size distribution.

The occurrence of each food was assessed by adding up the index of importance in individual guts (Owen, 1973). The index varies from + to 10, one point being allocated for each 10 per cent of the diet which was made up of a single food. Where a food constitutes less than 1% of the diet it is recorded as +. When indices are summed, two + values are counted as 1 index point.

Information on feeding behaviour was obtained from a series of long periods of observation in February 1970 and 1971. The proportion of the flock feeding was recorded at 10-minute intervals throughout the hours of daylight. The periods during which the head and neck were submerged when feeding were timed. These individual submergence times are termed 'feeding bouts'.

Results

Food

The vegetative contents of 30 swan guts are shown in Table 1, where foods are listed in order of importance. Since only two Whooper Swans were examined they are not discussed separately but are included in the total figures.

The oesophagi and gizzards of some birds that died of lead poisoning were distorted and crammed full of food. Jordan & Bellrose (1951) reported that this was a frequent occurrence in poisoned Mallard *Anas platyrhynchos*. Although food consumption by the ducks decreased in the latter stages, the

Table 1. Vegetative content of Ouse Washes swan guts. Leaves unless otherwise stated.

Washes Foods	Bewick's		Mute		All Swans		
	F	Index	F	Index	F	Index	% Index
Rorippa palustre roots	4	23	5	31+	10	63	23·2
Agrostis stolonifera	2	30+	3	9	11	46+	17·2
Alopecurus geniculatus	10		2		13		
Glyceria maxima leaves, stems, rhizome	8	38	2	1+	12	41	15·1
Poa trivialis	6	16	3	11+	9	27+	10·2
Glyceria fluitans	8	16	3	3	13	20+	7·6
Trifolium repens stolons	3	15	0	0	3	15	5·5
Unidentified stem, root	5	5+	0	0	6	6+	2·4
Agropyron repens	4	2+	0	0	5	5+	2·0
Callitriche sp.	0	0	2	5	2	5	1·8
Apium nodiflorum	0	0	1	5	1	5	1·8
Phalaris arundinacea	3	3	0	0	4	4	1·5
Equisetum sp. shoots	1	2	0	0	2	4	1·5
Ranunculus repens	2	1+	2	1+	5	3+	1·3
Deschampsia caespitosa	2	1	2	2+	4	3+	1·3
Dactylis glomerata	2	2+	0	0	2	2+	0·9
Filamentous green alga	2	1+	1	+	3	2	0·7
Ranunculus ficaria roots	1	2	0	0	1	2	0·7
Salix sp.	1	2	0	0	1	2	0·7
Lolium perenne	2	1+	0	0	2	1+	0·6
Potentilla anserina	1	+	1	+	2	1	0·4
Unidentified dicotyledon	2	1	0	0	2	1	0·4
Holcus lanatus	2	1	0	0	2	1	0·4
Senecio aquaticus rootstock	1	1	0	0	1	1	0·4
Ceratophyllum demersum	0	0	1	1	1	1	0·4
Polygonum amphibium rhizome	0	0	1	0	1	1	0·4
Plantago media rootstock	1	1	0	0	1	1	0·4
Plantago media	1	+	0	0	1	+	t
Ranunculus subgen. *Batrachium*	0	0	1	+	1	+	t
Unidentified grass	0	0	1	+	1	+	t
Carex sp.	1	+	0	0	1	+	t
Myosotis sp.	1	+	0	0	1	+	t
Potamogeton lucens	1	+	0	0	1	+	t
Total leaves	16	122	7	42	25	182	67·2
Total roots, stolons, stems	8	47+	5	31+	15	89	32·8
Total	16	170	8	73+	26	271	
Fen Foods							
Whole peas	3	21	0	0	3	21	
Potato tubers	3	12	0	0	3	12	
Winter wheat leaves	1	10	0	0	1	10	
Total	4	43	0	0	4	43	

weakening and partial paralysis of gizzard musculature prevented efficient grinding and passage of food, so many meals may be present. The inclusion of these guts in analyses based on weight or volume would bias the results, but the index of importance used here gives these guts the same weighting as others. There is no evidence that the diet of swans suffering from lead poisoning is exceptional.

The starchy roots of marsh yellow-cress *Rorippa palustre* contributed the most important single item and was taken by all species. Summer flooding of the washes in 1968 and 1969 resulted in many relatively bare, damp areas ideal for the growth of this plant. During a series of drier years that followed there was a progressive decline. Nine out of 16 swans which had fed on the washes before the end of the 1970–1971 winter contained *Rorippa* roots, but none of the 10 wash-feeding swans collected subsequently. The difference is significant (Chi-square $P < 0{\cdot}005$). Next in importance were the soft grasses creeping bent *Agrostis stolonifera* and marsh foxtail *Alopecurus geniculatus* which usually occurred together in guts and were not quantitatively separated because of identification difficulties. *Agrostis* is particularly widespread on the grazed washes, occurring in all but the wettest areas. The *Alopecurus* is associated with areas normally flooded for long periods in the winter and was locally abundant at several sites favoured by Bewick's Swans during the first two winters of the study. In the early winter, when there was little flooding, these swans grazed low-lying damp areas where floating sweet-grass *Glyceria fluitans* was dominant. This species and rough-stalked meadow-grass *Poa trivialis,* another soft grass favoured by swans, both grow actively in the autumn. *G. fluitans,* like the *Rorippa,* appeared to decrease on the washes following several dry summers and the 1972–1973 winter when there was little flooding. Reed grass *Glyceria maxima* was dominant over low areas of the Ouse Washes, particularly in lightly grazed or ungrazed washes. Though Bewick's Swans did not feed on its fibrous leaves and stems in the early part of the winter, this grass formed an important part of their diet later, particularly during periods of deep flooding and after the palatable new shoots emerged in February. The swans tended to avoid reed canary-grass *Phalaris arundinacea* and tufted hair-grass *Deschampsia caespitosa. Phalaris* was one of the most widespread and abundant grasses on the washes while the *Deschampsia* was plentiful in the higher areas but has particularly coarse leaves.

When Bewick's Swans fed on the flood banks they took white clover *Trifolium repens* stolons as well as the leaves of such grasses as rye-grass *Lolium perenne* and cocksfoot *Dactylis glomerata* which are confined to the better drained ground. Clover stolons and these grasses are common foods of Bewick's Swans in Gloucestershire (Owen, unpublished).

The proportions of different food groups used by swans when feeding on the washes are shown in Figure 1. The diet of the Mute Swan differs from that of the Bewick's in that there is a larger proportion of aquatic plants, such as starwort *Callitriche* sp., hornwort *Ceratophyllum demersum* and water crowfoot *Ranunculus* (sub-genus *Batrachium*) sp., which are associated with dykes. Bank plants were not represented in the guts of the Mute Swans examined. They cannot walk as well as Bewick's and are more reluctant to feed on land.

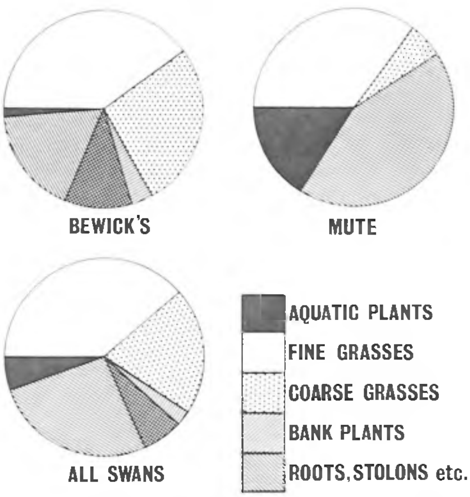

Figure 1. Main foods and habitats used by swans on the washes. The cross hatched area represents roots or stolons which occur only on banks (mainly stolons of *Trifolium repens*).

The seed constituents of the gut contents are shown in Table 2. Although seeds occurred in 58% of the examined swans which had been feeding on the washes they made only a minor contribution to the diet, as was concluded by Owen & Kear (1972). The quantity of seeds in single guts did however indicate some positive seed feeding by swans. The percentage by weight of seeds was 2·3% for Bewick's and 2·7% for Mute Swans. As seeds are retained for longer in wildfowl gizzards than green vegetation (Swanson & Bartonek, 1970; Owen, 1973) even these low

Table 2. Seed constituents of Ouse Washes swan guts.

	Bewick's		Mute		All Swans	
	F	D wt.	F	D wt.	F	D wt. (mgm)
Glyceria fluitans	4	24	2	38	6	62
Eleocharis sp.	3	3290	2	717	5	4007
Rumex crispus	3	17	2	15	5	32
Bait wheat	1	232	0	0	3	1772
Polygonum amphibium	1	22	2	34	3	56
Carex disticha	2	3	1	139	3	142
Carex riparia	2	25	0	0	2	25
Polygonum persicaria	1	13	1	2	2	15

Seeds occurring only once (mgm):
Bait barley (500), *Juncus articulatus* (30), *Atriplex hastata* (10), *Polygonum lapathifolium* (9), *Galium aparine* (8), *Hippuris vulgaris* (3), *Ranunculus repens* (3), *Bidens tripartita* (3), *Poa trivialis* (1), *Rumex palustris* (1), *Carex hirta* (1), *Trifolium repens* (1), Unidentified (1).

percentages exaggerate the importance of seeds. Corrections have been calculated for Wigeon feeding at the Ouse Washes by comparing gizzard contents with those of the rectum (Owen, unpublished). If these corrections hold true for swans, whose main foods resemble those of Wigeon, seeds would actually make up only 0·03% of their overall diet. Of the seeds taken by swans, those of spike-rush *Eleocharis palustris* were the most important when assessed by dry weight but they only occurred in five of the birds examined. *Eleocharis* seeds form a large proportion of the food of several species of ducks on the Washes (Thomas, 1975a).

Animal material was recorded in three Bewick's Swans. One contained a single coleopteran (beetle) larva, and one had two dipteran (fly) larvae and 3 beetles of 3 families. The third swan, which had fed on a wide variety of bank plants including clover stolons, contained adult beetles of three families, a beetle larva, a dipteran larva and pupa, one spider, a large flea and one oligochaet worm. All the beetles ingested were common ground beetles mainly of the families Carabidae and Cerambycidae. All animals had probably been ingested incidentally.

The weight and size distribution of grit in swan gizzards are shown in Table 3. In common with other grazing wildfowl (Anderson, 1959; Owen, 1973, and unpublished), both Mute and Bewick's Swans selected sand and gravel of relatively small particle size, over 90% by weight being less than 2 mm in diameter. This is probably more effective at puncturing leaf cells than the larger gravel taken by those ducks which are mainly seed eaters. Though there are several gravelly spoil heaps near the banks the surface soil at the Ouse Washes is deficient in grit since it is largely composed of peat and fine silt.

Table 3. Grit content of swan gizzards.

	Bewick's	Mute
No.	13	7
Mean wt.	28·5	69·8
Range	8·3–65·9	32·8–153·0
% > 2 mm	9·9	6·9
% > 1–2 mm	48·1	29·5
% > 0·5–1 mm	31·4	46·1
Less than 0·5 mm	10·6	17·5

From 1971 grain was supplied to attract the swans into the lagoons in front of the Wildfowl Trust observatory at the Welney refuge. Large numbers of swans came to the lagoons, which they also used as a roost (Cadbury, 1975). At first the amount of food was increased as the number of swans increased. In 1974–1975 about half of the quantity put out the previous season was put out in a deliberate attempt to keep the numbers of swans using the Welney lagoons (as opposed to the rest of the Ouse Washes) to a few hundreds.

The proportion of time spent by swans at the Welney refuge over the five seasons is shown in Figure 2. Swan usage increased

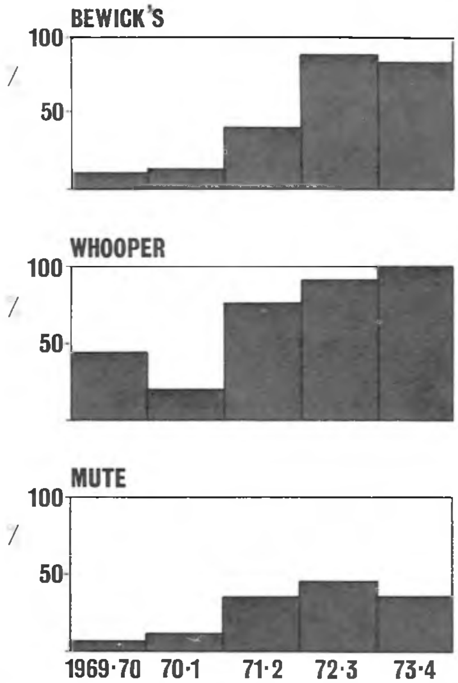

Figure 2. The proportion of swans using the Wildfowl Trust's Welney Refuge expressed as a percentage of total swan days on the Ouse Washes, 1969–70 to 1973–74.

during the period, although in 1974–1975 the area was used largely as a roost.

The use of fenland (the arable fields outside the washes) for feeding is shown in Table 4. This was first recorded in February 1970 when the washes were not only extensively flooded but also frozen. When the washes were flooded in the following winter Bewick's Swans again resorted to feeding on fenland but this habit did not become regular until the later half of the 1972–1973 winter when there was exceptionally little flooding. Once established the habit has persisted, irrespective of conditions on the washes. The fields used have all been within 3 km of the washes.

Of the Bewick's Swan guts examined, only four were from birds which had been feeding on fenland, and three were from the same period in March 1974. These three had fed on peas and potato tubers and the other contained winter wheat leaves. Table 4 provides a more adequate picture of the seasonal pattern in the foods taken in the fens. In two successive winters Bewick's Swans fed on one of the few pastures adjoining the washes. Sprouting wheat was usually only available in the stubbles for a short period before they were ploughed. Waste potatoes, on the other hand, remained a source of food for much longer. Large quantities of tubers lay on the surface after the harvest and again following the autumn ploughing. Only the smaller ones were eaten by swans until the others became frosted. In 1973–1974 winter swans frequented fields from which sugar beet had been harvested. The birds took both waste fragments of beet and 'weed' potatoes, quantities of which were exposed when the sugar beet was lifted. In 1974 the beet harvest and ploughing were delayed by the water-logged state of the fields. Entire sugar beet roots are too hard for the bills of ducks (Thomas, 1975a) but can be managed by Pink-footed Geese *Anser brachyrhynchus* (R. Berry, pers. comm.), while Whooper Swans are known to eat sound turnips in Scotland (Kear, 1963). Bewick's Swans did not eat sound beet roots in the fens. The peas found in the guts had

Table 4. Records of Bewick's Swans on agricultural land near the Ouse Washes.

	Grass ley Swans			Sprouting wheat in stubbles Swans			Waste potatoes Swans			Waste sugar beet and potatoes Swans			Winter wheat Swans		
	Fields	Av.	Max.	Fields	Av.	Max.	Fields	Av.	Max.	Fields	Av.	Max.	Fields	Av.	Max.
1969–70		—			—			—			—		1	50	
1970–71		—			—		1	39			—		2	110	150
1971–72		—			—			—			—			—	
1972–73		—			—			—			—		5	60	102
1973–74	1	100		4	27	40	6	96	320	1	66		6	130	300
1974–75	1	100		1	400		3	304	691	2	405	560	5	205	480
Period		Nov.			Nov.–Dec.			Nov.–Feb.			Dec.–Jan.			Feb.–Mar.	

probably been taken from the surface of a recently drilled field.

In the spring Bewick's Swans turned to grazing the shoots of winter wheat, which frequently follows potatoes in the fenland farm rotation. The first record of Bewick's Swans feeding on winter wheat appears to be with Whooper Swans in Roxburghshire in 1968 (MacMillan, 1969). Carrots and winter wheat were among the foods taken by this species at the Wexford Slobs, Ireland, though waste potatoes also formed a major part of the diet there (Merne, 1972). The only recorded instance of Bewick's Swans feeding on carrots near the Ouse Washes was a few birds in December 1974.

Feeding behaviour

Bewick's Swans fairly frequently grazed in the washes up to 100 m from the water's edge. They also grubbed roots or rhizomes from the mud. When Mute Swans grazed on land this was largely in the spring and they plucked grass from the banks of rivers and dykes while swimming.

When floating on water all three species most frequently adopted the dipping method of feeding, immersing the head and neck. The mean lengths of single dipping bouts are given in Table 5. These compare with recorded values of 15–20 seconds for Bewick's (Acland, 1923), an average of 9·3 seconds for Mute (Dewer, 1942) and 10–20 seconds for upending Whooper Swans (Airey, 1955). Bout lengths by upending tend to be longer than dipping bouts.

The reach of swans was measured from the tip of the bill to the anterior end of the sternum (dipping) and the junction of the legs with the body (upending). Adult Mute Swans could feed by dipping at a depth of 79 cm (n = 5) and by upending to 103 cm (n = 2), adult Bewick's Swans at 59 cm (16) and 84 cm (3). Cygnets of Bewick's could reach 56 cm (7) and 77 cm (3). In late January 1975 when flooding was very deep Mute Swans remained on the washes while many Bewick's were forced to leave (see Cadbury, 1975). Swan families frequently fed on the landward side of flocks, possibly because the smaller cygnets were only able to feed in shallower water.

The feeding activity of over 100 Bewick's and more than 30 Mute Swans, recorded in the same area over a few consecutive days in February during cold weather, is shown in Figure 3. All fed by dipping while floating in water. Both species increased their feeding activity through the day, but a plateau was reached three hours after sunrise in Mute Swans and six hours after sunrise in Bewick's. In both species this level was reached when 70 to 80% of the birds were feeding. This level remained constant until dusk. Car headlights flashed on to the water indicated that intensive feeding continued up to one hour after dark, but an hour later most were resting. Bewick's Swans fed for a total of approximately 6·3 hours. The mean feeding activity expected if every bird had feeding bouts followed by intervals, both of which were of the mean lengths given in Table 5, is 71% for Bewick's and 76% for Mute Swans. This agrees well with the recorded plateau and can be regarded as the average maximum feeding activity for swan flocks on water. Data collected in January 1970 following a period of intensive disturbance shows that this level can occasionally be exceeded in Bewick's. Over the first six hours after sunrise (records at 20 minute intervals) an average of 87% of the birds were feeding. If the average bout length were constant, at 9·6 seconds, the interval between bouts would have been reduced to 1·4 seconds. It is likely therefore that these swans were feeding in longer bouts as well as reduced inter-bout times. These

Table 5. The dipping action of swans when feeding in water.

	Mute	Bewick's	Whooper (deeper water)
Mean time			
Head submerged (secs)	8·9 ± 3·3	9·6 ± 4·3	8·2 ± 4·5
Number of observations	51	81	57
Mean time			
Head above water (secs)	2·8 ± 1·6	4·0 ± 3·0	6·3 ± 6·3
Number of observations	9	33	25

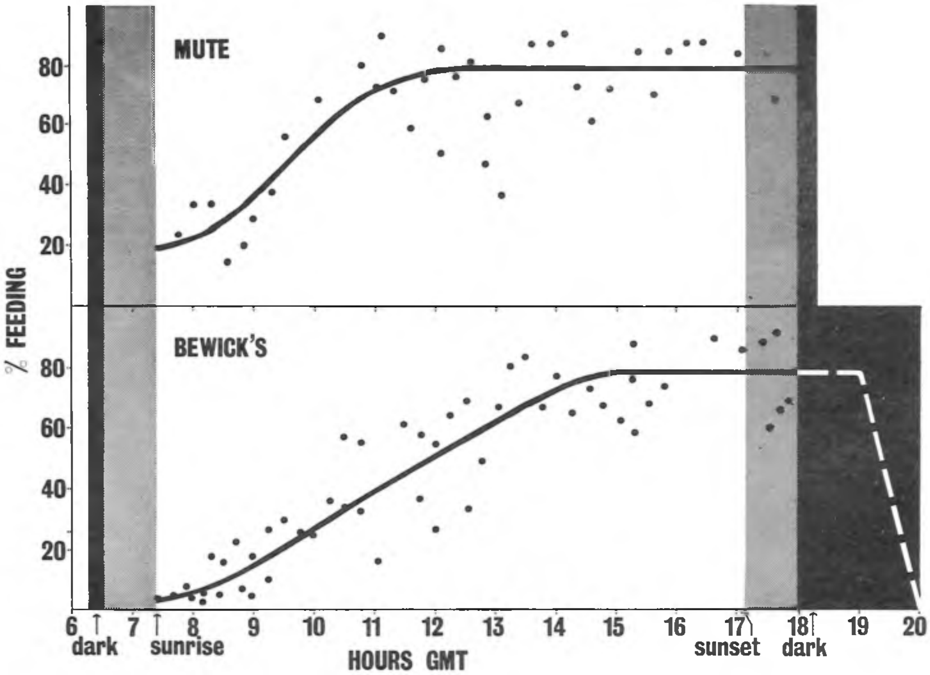

Figure 3. The proportion of swans feeding in relation to time of day, February 1970. All swans were feeding from water.

birds also altered their feeding rhythm and probably fed for a larger proportion of the day.

The rhythm described is different from that of wildfowl such as geese (Owen, 1972) and dabbling ducks (Thomas, 1975a). Wildfowl feeding on land are mainly diurnal feeders because of the risk of predation after dark and because they rely on sight for feeding. Swans feeding from water use touch to a greater extent than sight to select their food (Owen & Kear, 1972) and are safe from land predators. On fenland their activity resembles that of geese, feeding intensively in the morning and afternoon, resting in midday and returning to the roost (on the washes) at night. Swans which supplemented their diet with grain at the Welney lagoons fed for an average of only 10–25% of their daytime (including periods of grazing) with peaks corresponding to times when food was put out. These birds spent most of their time sleeping or swimming (Wager, 1974).

Roosting

When the washes were flooded the swans normally roosted on the internal dyke banks when these were surrounded by water or were shallowly submerged. When there was little flooding or the area was frozen the birds used one of the rivers bordering the washes as a roost. Occasionally, where there was excessive disturbance from wildfowling, groups of up to 140 Bewick's Swans spent the night at local gravel pits. Since the 1971–1972 winter, most of the Bewick's and Whooper Swans at the Ouse Washes, as well as many Mutes, have roosted at the lagoons created by the excavation of shielding banks on the Welney refuge. Many of the birds used the lagoon edges and islands close to the observatory where they were illuminated by floodlights from dusk to 10 p.m. The swans feeding on farmland flighted back at dusk to the security of the refuge.

Mortality

During the six winters between 1969 and 1975, 128 swans were found dead at the Ouse Washes. Since these birds probably represented a large proportion of the swans which died over the period an attempt is made to calculate overall winter mortality using the average population present over the

Table 6. Percentage winter mortality of swans at the Ouse Washes, 1969–75.

	Mute	Whooper	Bewick's
More than 1 year old	2·5	—	1·2
Cygnets	4·5	—	2·4
Overall	3·0	3·0	1·4

December–February period, 1969–1975 (Table 6). Among both Mute and Bewick's Swans a higher proportion of cygnets died than of older birds.

The cause of death, where this was ascertained, is shown in Table 7. The high percentages of casualties from collisions with power lines (33% for Mute and 43% for Bewick's Swans) are not unexpected since 44% of the deaths of Mute Swans in Britain for which the cause was known resulted from such collisions (Ogilvie, 1967). One 400 kv transmission line crosses the washes just north of the Welney refuge. A lower voltage line that spanned the refuge was removed in 1970, but there are still at least six others crossing the length of the Ouse Washes. Multiple collisions with power lines by Bewick's Swans have been recorded on four occasions. Three of these involved birds flighting between fenland feeding grounds and the washes. After frost swans leave the fields encumbered by soil adhering to their feet. Three Bewick's Swans were killed by striking obstacles other than power lines. The proportion of Bewick's Swan cygnets involved in collisions (Table 7) was 29%, considerably higher than the average percentage of cygnets over the 1969–1975 winters (15%). There was a similar trend among Mute Swans (31% compared with 23%) although Ogilvie (1967) found only a small difference in the vulnerability of first year Mute Swans to collisions but an appreciably higher proportion of second year birds hit wires.

At least 3,500 wildfowl, including 150 Bewick's Swans are known to have died as a result of an oil spillage on 27th December 1970 which affected the Biesbosch wetland in the Netherlands (Belterman, 1971). Following this incident a minimum of 24 Bewick's and four Whooper Swans that were contaminated with oil were seen at the Ouse Washes between 2nd January and 30th March 1971. Two of the

Table 7. The causes of death of swans on the Ouse Washes, 1969–75.
Numbers of cygnets in brackets.

	Mute	Whooper	Bewick's	Unident.	Total	% of total deaths
Power lines	17(5)	2(1)	28(8)	2(1)	49(15)	38
Other collisions	0	0	3(2)	0	3(2)	2
Probably shot	3(0)	0	7(3)	0	10(3)	8
Oiling	0	0	2(0)	0	2(0)	2
Lead poisoning						
—known	2(0)	1(0)	7(0)	0	10(0)	
—calculated					37	29
Total known	22(5)	3(1)	47(13)	2(1)	74(20)	
Unknown	30(13)	2(0)	18(4)	4(1)	54(18)	
Total	52(18)	5(1)	65(17)	6(2)	128(38)	

Notes: Total deaths from lead poisoning are extrapolated from autopsy data.
Percentages in the right hand column do not add up to 100. The remaining 11% is probably distributed through the stated categories, rather than being from unrecognised causes.

Table 8. Incidence of ingested lead and symptoms of poisoning in Ouse Washes swans.

	No. examined	Ingested shot	Fishing weights	All lead	Poisoning symptoms	Probable cause of death
Bewick's A	19	7	3	9	9	7
J	6	0	0	0	0	0
Whooper A	1	1	0	1	1	1
J	1	0	0	0	0	0
Mute A	7	3	3	5	4	2
J	1	0	0	0	0	0
Total Adults	27	11	6	15	14	10
Juveniles	8	0	0	0	0	0
Overall	35	11	6	15	14	10

heavily oiled Bewick's Swans died.

The occurrence of lead pellets and finishing weights in the gizzards of the 35 birds autopsied and the number of deaths attributed to poisoning is given in Table 8. None of the eight juvenile swans contained pellets in the gut or died of poisoning, but 15 out of 27 adults (56%) had ingested lead and the deaths of 10 of these were definitely attributed to lead poisoning. The 29% poisoned can be taken as a minimum estimate of deaths from this cause. This being so, an estimated 37 swans died from lead poisoning at the Ouse Washes over the six winters.

Both Mute and Bewick's Swans, including three out of the seven adult Mutes examined, contained ingested fishing weights. These are distinguished from pellets by their flattened appearance and they sometimes have steel loops attached. Mute Swans, which frequently feed along heavily fished water courses in the vicinity of the Ouse Washes are liable to ingest weights with vegetation. In addition to birds dying of poisoning, five out of seventeen adult swans known to have died from other causes contained ingested lead and four of these showed symptons of poisoning. Bellrose (1959) has shown that poisoned birds are more vulnerable to shooting because their flying ability is impaired, and poisoning may cause more deaths than is apparent from Table 7.

Discussion

Between 1969 and 1975 the Bewick's Swans at the Ouse Washes exhibited considerable flexibility in exploiting three distinct food resources. The reasons behind the two major changes, from natural vegetation on the washes to grain, and since the 1972–1973 winter, to feeding on agricultural land merit further discussion. These changes also had implications on the survival of the swans.

The increase in usage of the Ouse Washes (Cadbury, 1975) may have induced Bewick's Swans to explore new habitats. Once a habitat is established its spread through the population is facilitated by the birds' gregariousness. The Whooper Swan and Pink-footed Goose are among several species of wildfowl that have changed their feeding habits to exploit food sources on farmland in the present century (Kear, 1963, 1965). More debatable are the factors which influence the initiation of a change.

Deep flooding and absence of flooding prevented Bewick's Swans from obtaining their food on the washes and prompted them to seek other sources, often in situations where disturbance was considerable. Not only was the grain provided on the Welney refuge where the birds could feed undisturbed when the washes were flooded, but it has a higher energy value than wetland grasses. Moreover, the recent decline of *Rorippa palustre,* the roots of which have a high starch content and were prominent in the diet of swans before the end of the 1970–1971 winter, may have induced birds to search for high energy substitutes. It took only one winter before most of the Bewick's Swan population wintering at the Ouse Washes were supplementing their diet with grain.

Mattiasson (1973) calculated food consumption of 0·077 kg dry weight of *Zostera* per kg body weight per day for moulting Mute Swans. If the same holds for Bewick's, whose body weight averages about 6 kg, the daily dry weight consumption would be 0·46 kg dry, or just over 2 kg fresh weight of grass. The real value is likely to be slightly larger than this because smaller birds need more energy per unit weight than large ones. There is little doubt that there is enough vegetation on the washes to support larger numbers of swans than the area has hitherto held. However during the shooting season the availability of this vegetation is severely limited by shooting and associated disturbance. The 304 ha (750 acre) Welney refuge is the only contiguous undisturbed area large enough to attract large numbers of swans for extended periods. Most of this refuge is heavily grazed by cattle in the summer in order to provide short grass suitable for Wigeon, and the area does support up to 2·2 million Wigeon days, mostly during the shooting season from September to January. This leaves little longer vegetation suitable for swan feeding.

The grain provided was not intended fully to support all the swans using the refuge but to draw them in for close observation. In 1973–1974 the total amount of grain fed during the season was sufficient for only 44,000 swan days, whereas more than 100,000 swan days were spent on the refuge (though many of these for roosting only). The amount of grain was reduced in 1974–1975 to provide for about 25,000 swan days. In this season the number of swan days (including roosting) was 75,000. Thus the creation of a refuge at Welney and its rapid adoption as a feeding place and roost by large numbers of swans probably resulted in an increase in the usage of the washes as a whole and may have contributed to the recent trend towards fenland feeding. With the safe roost at Welney enabling swans to feed on nearby arable land, the carrying capacity of the washes and surrounding fenland seems far from limiting.

Increasingly, damage to agricultural crops is being attributed to wildfowl. Whooper Swans on arable farmland in Scotland (Kear, 1963) and Bewick's Swans in Wexford (Merne, 1972) appear to have largely fed on waste crops and this applies to Bewick's Swans for much of the winter near the Ouse Washes. The grazing of winter wheat has brought some complaints when their large webbed feet could cause damage by puddling. However, the Bewick's Swans leave the wintering grounds too early for substantial damage to occur. The yield of winter wheat was unaffected by two weeks of grazing by swans in January 1972 (Thomas, pers. comm.). There is no evidence that swans dig up seeds or pull up sprouting wheat.

These changes in food sources are probably beneficial to the swans' nutrition but they may increase winter mortality. The flighting of swans between the washes and farmland increases their vulnerability to collisions with power lines, several of which cross the fens where the birds feed.

Jordan & Bellrose (1950) emphasize the importance of diet in susceptibility to lead poisoning. They showed that whereas 60–80% of Mallard on a cereal or seed diet died on ingesting one pellet, few birds on a diet including plant leaves succumbed. The effect was so marked that only two out of six ducks, each dosed with 25 pellets, and feeding on leafy matter, died. Thus the incidence of deaths from poisoning may increase among swans which supplement their diet with grain.

Although Godin (1967) found from experiments with captive birds that the mortality of lead-poisoned Mallard was not affected by the amount or type of grit available, birds searching for grit in areas where it is deficient, such as the Ouse Washes which have been heavily shot, must encounter and ingest lead pellets frequently. Most of the grit in the swan gizzards was highly polished and had been held there for some time, suggesting that the birds were not able to supplement their grit during the winter. Hoffmann (1960) found that the incidence of lead in the gizzards of Tufted Ducks *Aythya fuligula* was reduced from 40% to 5% after scattering grit on the feeding habitat in the grit-deficient Camargue, France. In 1974–1975 the Wildfowl Trust provided grit for swans on their Welney refuge and this may partly alleviate lead poisoning problems in future.

Among the ducks at the Ouse Washes the incidence of lead poisoning is lowest in the Wigeon which largely feeds by grazing the leaves of grasses (Thomas, 1975b). There is considerable overlap between the food of this species and the swans, particularly Bewick's, but since the latter also grub for roots of such plants as *Rorippa palustre* on the washes they are more liable to ingest shot.

Lead poisoning has not often been recorded as a cause of death of wild swans in Britain. The only Whooper Swan examined by Macdonald (1962) had died of lead poisoning. Ogilvie (1967) recorded no poisoning deaths in Mute Swans but none of these was examined internally. In his sample some of the 51% which died of unknown causes probably were poisoned by ingested lead. Lead poisoning was found to be an important mortality factor in Whistling Swans *Cygnus c. columbianus* in Ontario (Irwin, 1975).

In spite of legislation protecting all species of swans, Bewick's Swans were shot, perhaps some times in mistake for geese. Over the six winters at least seven were suspected as having been killed by shooting and others were wounded. 'Pricked' birds were present in most summers. Evans *et al.* (1973) recorded that 34% of all Bewick's Swans X-rayed alive at Slimbridge carried lead pellets in their tissues. Lead pellets in the tissues (as well as those ingested) may increase the vulnerability of swans to collisions in flight. A Mute Swan which died from striking power lines carried no fewer than 24 pellets. A Bewick's Swan which collided with the Welney observatory had previously been shot in the wing.

The overall mortality of Bewick's Swans during winter, at 1·4%, appears low. This occurs however during only a third of the swans' year whereas the major hazards of two long migrations and the stresses of breeding occur during the other two-thirds. Moreover, recruitment to the population is low, only 15% per annum in recent years. Deaths from lead poisoning might appear lower than they are, if, as is likely, birds on passage or individuals visiting the washes for short periods in midwinter ingested shot and died elsewhere. Any measures likely to reduce mortality, such as supplying grit, feeding less grain or removing overhead wires would make a useful contribution to the future success of this population.

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Summary

The ecology and feeding behaviour of Mute *Cygnus olor,* Whooper *C. cygnus cygnus* and Bewick's Swans *C. columbianus bewickii* over six winters 1969–1975 at the Ouse Washes, England, is described. An analysis is made of the winter mortality of swans at the site.

The swans exploited three distinct food sources during the period: natural vegetation on the washes, grain which was specially provided and crops, particularly waste potatoes, on adjoining farmland. When feeding on the meadows, swans preferred soft grasses, *Agrostis stolonifera, Alopecurus geniculatus* and *Glyceria fluitans,* to the coarser species also available. *Glyceria maxima* was, however, an important late winter food. The starchy roots of *Rorippa palustre* were a prominent constituent in the diet in the first two winters after which the plant decreased. Seeds of wetland plants and animal material made an insignificant contribution to the diet. Once supplementary feeding with grain started a large proportion of the swans made use of it. Since the 1972–1973 winter many Bewick's Swans have fed on waste crops, particularly potatoes, on neighbouring fenland farms. It is suggested that the change was brought about by increase in swan usage following the creation of a large undisturbed refuge, and possibly by the birds searching for high-energy foods to replace declining *Rorippa.*

Undisturbed swans on water increased their feeding activity during the day and continued to feed after dark. By contrast, when on farmland swans fed intensively in the morning and later afternoon with a period of relatively low activity at midday.

On average about 3% of the Mute and Whooper Swan population and 1·4% of the Bewick's Swans at the Ouse Washes died each winter. Collisions with power lines (30%), poisoning from ingested lead pellets and fishing weights (29%) and shooting (8%) accounted for most of the deaths of 128 swans recorded over six winters. Birds are likely to ingest lead pellets as grit in this grit deficient area and the provision of grit in feeding areas or roost might lessen deaths from poisoning. Although the changes in diet are probably beneficial to the birds' nutrition, grain-feeding increases susceptibility to death from lead poisoning and flighting to and from the fenland farms increases mortality from collisions with power lines.

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