Populations of swans at the Ouse Washes, England

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Introduction

The Ouse Washes which extend from Cambridgeshire into Norfolk were recognized by the British Government when it signed the Ramsar Convention in September 1973 as being one of the 13 wetlands in the United Kingdom which were of international importance (White Paper, Cmnd. 5483, December 1973). In the six winters 1969–1975 the area supported a mean maximum of 53,000 wildfowl, a population exceeded by no other inland site in Britain and Ireland. It is one of 19 in Britain and Ireland which has had at least 1% of the north-west European population of one or more species of wildfowl in January since the International Counts began in 1967 (Atkinson-Willes, in press). At the Ouse Washes this criterion was reached for four species of dabbling duck but it is for the Bewick's Swan *Cygnus columbianus bewickii* that the area is outstanding.

Little is known about the swans of the region before the main draining of the Fens in the first half of the 19th Century. Judging by bones in post-glacial peat deposits, the Whooper Swan *C. cygnus cygnus* was frequent in the Cambridgeshire Fens about two thousand years ago (Milne-Edwards, 1868). However, no remains of the Bewick's Swan have so far been identified in the area (M. Northcote, pers. comm.). Lack (1934) knew of only six records of Bewick's Swans in Cambridgeshire and none was recent. Nisbet (1955) and Ogilvie (1969) have reviewed the changes that took place in the Bewick's Swan population at the Ouse Washes up to 1968 and discussed some of the factors influencing these changes. The Mute Swan *C. olor* was almost certainly first reduced to a state of semi-domesticity in the Fenland (which included the area now occupied by the Ouse Washes) and during the second half of the 15th Century and the 16th Century the keeping of swans was well organized there. Extrapolating from 'upping' figures the Mute Swan population of the Fenland was at least 24,000 birds in this period (Ticehurst, 1957).

In addition to populations this paper covers usage of the Ouse Washes by swans, their distribution both within the Ouse Washes and in surrounding areas, and productivity. Feeding ecology and mortality are considered in a separate paper (Owen and Cadbury 1975).

Methods

Between September and April of the study period 1969 to 1975, the swan populations were counted and mapped at least once a month over the 32 km length of the Ouse Washes. For the first three winters the censuses were carried out twice monthly between November and March. For convenience the the Ouse Washes were divided into five sectors: Earith, including Berry Fen (the furthest upstream)—Mepal— Purl's Bridge—Pymore railway viaduct—Welney—Welmore Sluice (see Figure 1). Records were kept of the proportions of cygnets for all three species and brood sizes of Whooper and Bewick's Swans. The potential breeding population of Mute Swans was censused each year 1970—1974. Information on flood levels and periods of freezing for the winters 1968–1974 was collected as part of the Royal Society for the Protection of Birds' research programme at the Ouse Washes. For information prior to 1968 on swan populations, flooding and freezing, reference was made to the Cambridge Bird Club Reports.

Between 1960 and 1969 about 400 Mute Swans were ringed at Cambridge and at Earith at the south-west end of the Ouse Washes by C. D. T. Minton, C. J. Reynolds and others. Ringing recovery data were extracted from the British Trust for Ornithology's ringing recoveries.

Habitat and land usage at the Ouse Washes

The Ouse Washes are fields divided by ditches, many of which are overgrown and silted up. Between May and October most of the fields are grazed by livestock. Apart from the ditches and drains there is little permanent water on the washes, though conservation bodies and wildfowlers have created a number of pools in recent years.

In winter excess water from the River Ouse and surrounding farmland is diverted on to the Ouse Washes via the Old Bedford River and Delph (Figure 1). The water floods across the width of the washes at least once most winters, usually after the New Year. More details are supplied by Cottier and Lea (1969) and Thomas (in prep.).

The total area of the Ouse Washes is 1,941 ha, 1,100 ha (57%) of which have been acquired by the Cambridge and Isle of Ely Naturalists' Trust, the Royal Society for the Protection of Birds and the Wildfowl Trust. Though there was no wildfowling over most of this land, shooting on neighbouring washes caused disturbance which greatly reduced usage of certain washes by wildfowl. There were, however, two sizeable blocks maintained as refuges. The RSPB's lay between Purl's Bridge and Pymore railway viaduct (203 ha). The Wildfowl Trust's, north of the Welney road (304 ha), was completely free of shooting and protected from disturbance over much of its length by an inner shield-bank.

Bewick's Swan

The international importance of the Ouse Washes for the Bewick's Swan

The small world population winters in two discrete areas, one in East Asia and the other in North-west Europe (Ogilvie, 1972). Apart from about 1,600 in Japan (IWRB Bulletin No. 36, December 1973) the number in the East is unknown. Not more than 7,000 winter in Europe. In the winter of 1955–1956, the great majority of this number were concentrated on the IJsselmeer polders in November (Nisbet, 1959), but the highest number counted in the January International Wild-

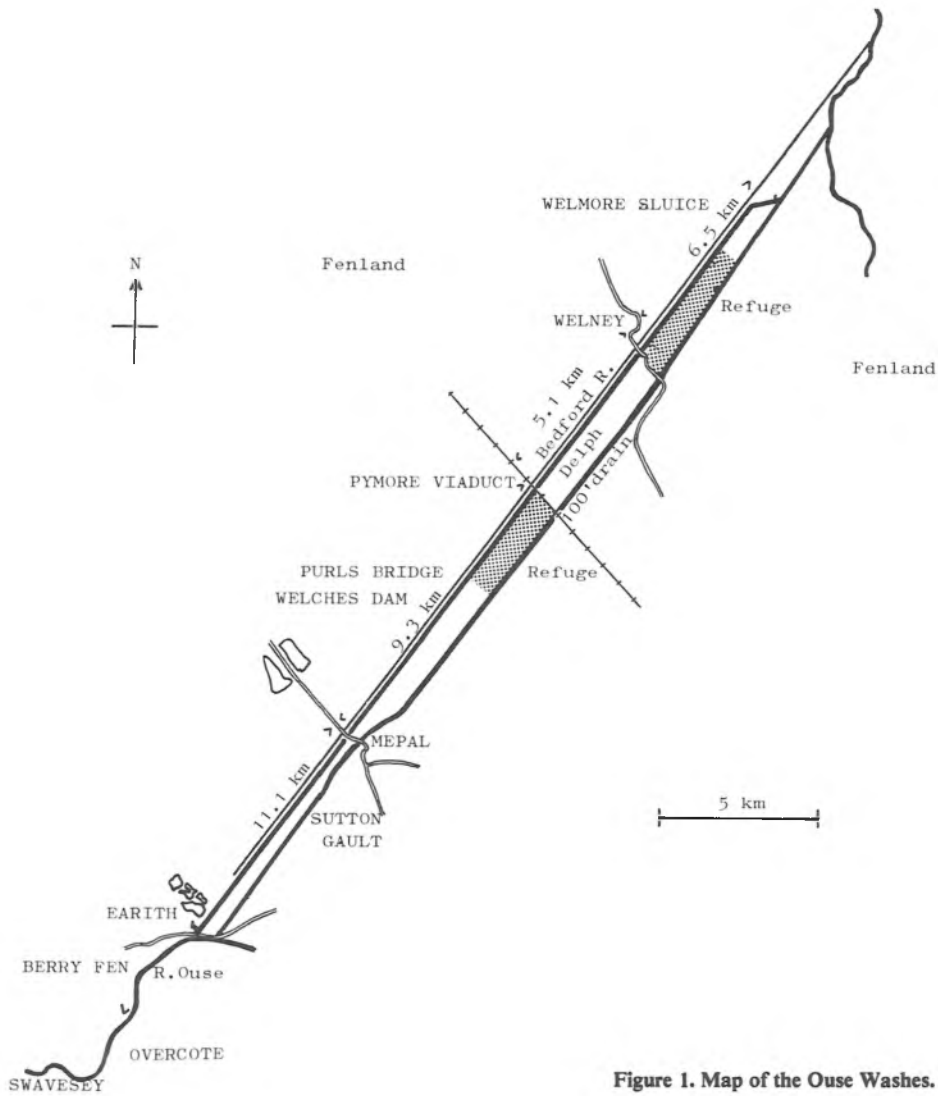

Figure 1. Map of the Ouse Washes.

fowl Counts since 1967 has been 5,871 in 1973 (Atkinson-Willes, in press). In at least two of the eight years to 1973 a total of 15 sites in north-west Europe held a January population of more than 1·5% of the western winter population (100 Bewick's Swans) but only 5 sites exceeded 5% (350). These were Slimbridge on the Severn estuary and the Ouse Washes in England, and three sites in the Netherlands. In Ireland, Loughs Neagh and Beg were probably in this category but there have been no complete counts of the swans there since 1967. Moreover, the population wintering on the Wexford Slobs has increased in recent years to about 300. Several other sites, particularly in the Netherlands and Germany, held more than 350 Bewick's swans in autumn and spring.

Taking the average highest count of Bewick's Swans in January over the years 1970–1975, the Bewick's swan population at the Ouse Washes in mid-winter not only represents 45% of those in Britain and Ireland but about 14% of the north-west European population (Table 1).

Winter maxima and usage of the Ouse Washes by Bewick's Swans

The mean winter maxima for Bewick's Swans at the Ouse Washes over the 1964–1975 period (814 ± 357) was significantly higher than that in 1952–1964 (301 ± 208). Inadequate coverage of the Ouse Washes prior to the 1952–1953 winter invalidates comparisons with earlier years. The highest number recorded on any date was 1,280 in February 1972. The population at the Ouse Washes exceeded 350 in only two winters between 1952 and 1964. In the subsequent period, however, more than 350 were recorded in 10 out of the 11 winters and in three the maximum exceeded 1,000. In nine out of the 22 winters the highest count has been in the second half of February.

An assessment of population usage of an area (expressed as swan days) avoids the bias resulting from an influx of transient birds if maximum numbers are used (Table 2). The mean usage by Bewick's Swans over the five winters 1969–1974 was more than four times

Table 1. The relative national and international importance of the swan populations at the Ouse Washes.

	Ouse Washes (mean max: Jan) 1970–75	Britain and Ireland	North-west Europe
Bewick's Swan	890	2,000	6,500
		45%	14%
Whooper Swan	31	4,500	14,000
		0·7%	0·2%
Mute Swan	294	24,000	132,000
		1·2%	0·2%

British and Irish and north-west European data—Ogilvie (1972).

Table 2. Mean usage of the Ouse Washes by swans.

	1954–1959	1959–1964	1964–1969	1969–1974
Mute Swan days	17,250		26,080	30,790
1 Dec–15 March	(3 winters)		(5)	(5)
	100%		151%	178%
Whooper Swan days		420	630	2,280
1 Oct–31 March		(4)	(5)	(5)
		100%	150%	543%
Bewick's Swan days	18,940	16,060	37,750	80,660
1 Oct–31 March	(5)	(5)	(5)	(5)
	100%	85%	199%	426%

higher than in the 1954–1959 period. The increase was more marked after 1964–1965 (Figure 2) when the mean usage in winter rose significantly from 37,750 ± 21,430 (1964–1969) to 80,660 ± 22,970 (1969–1974) Bewick's Swan days. Not only did larger numbers of swans visit the Ouse Washes but the time spent in the area increased. There has been a tendency for Bewick's Swans to arrive in substantial numbers earlier. Before the 1964–1965 winter an average of 15% of the total winter usage came before the end of December. Subsequently the average has been 25%.

Factors influencing the wintering populations of Bewick's Swans

Many of the fluctuations within a winter and in usage in different winters since 1946–1947 can be interpreted in terms of flooding at the Ouse Washes and periods of freezing (Table 3). Deep and extensive flooding (3 winters) and freezing (6 winters) deprived swans of areas where they could feed and they tended to move elsewhere or, as in recent years, fed on nearby farmland. The Bewick's Swan population was more affected by flooding and freezing than the Mute Swan (Figure 3). Usage by swans tended to be low if there was little flooding (4 winters), largely because passage birds did not remain on the washes. In recent years the high winter usage has been associated with moderate flooding and generally mild weather (5 winters).

About 2,000 Bewick's Swans (30% of the population in north-west Europe) have wintered in the Netherlands and Belgium since 1967 (Atkinson-Willes, in press). In severe weather the freezing of fresh-water areas in these countries sent large numbers of Bewick's Swans to Britain and Ireland (5 winters). The influxes of the 1954–1955 and 1955–1956 winters are discussed by Nisbet (1959). There was an unusually cold period on the Continent in both winters but in 1954–1955 deep flooding and freezing of the Ouse Washes reduced the usage of the area by Bewick's Swans displaced from the Netherlands. In the 1960–1961 winter the cold weather on the Continent did not spread over into eastern England where unfrozen water was available for the swans. Ogilvie (1969) suggests that these birds remained at the Ouse Washes rather than flying on to Ireland as they may have done previously in such circumstances. The high usage of the Ouse Washes by Bewick's Swans in the 1973–1974 winter may also in part be explained by cold conditions on the Continent causing an exodus of birds. In the 1956–1957 winter, when there was a relatively low usage of the area by Bewick's Swans, there was particularly mild weather on the Continent. Though more Bewick's than usual remained

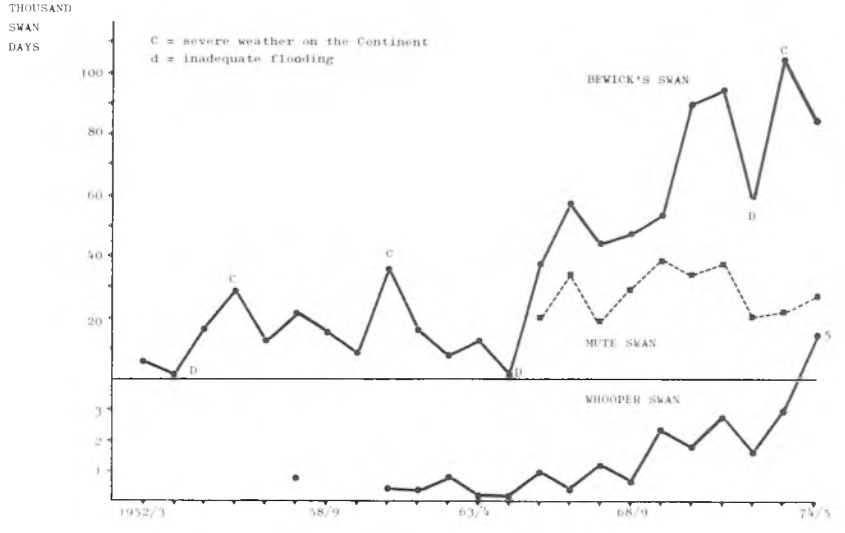

Figure 2. Winter usage of the Ouse Washes by swans.

Bewick's and Whooper: October–March. Mute: 1st December–15th March only.
C = severe weather on the Continent. D = inadequate flooding.

Table 3. Factors influencing Bewick's Swan populations at the Ouse Washes.

	Effect on Ouse Washes population	Winters
Depressing influence		
Flooding excessive	Swans displaced	1954–55, 1959–60, 1970–71 (Figure 3)
Flooding inadequate	Swans not arrested. Low usage. Small population. Jan. and Feb.	1953–54, 1964–65, 1972–73, 1963–64
Ouse Washes frozen	Swans displaced	1954–55, 1962–63, 1969–70 (Figure 3), 1958–59 (Jan.), 1959–60 (Jan.), 1961–62 (Dec.)
Mild winter on Continent	Relatively low usage	1956–57
Elevating influence		
Cold weather on Continent	Influx at Ouse Washes (Influx of Whooper and Mute Swans)	1946–47, 1954–55, 1955–56, 1941–42
Cold on Continent but relatively mild at Ouse Washes	Relatively large population and high usage	1960–61, 1973–74
Mild winter and moderate flooding	Relatively high usage	1965–66, 1966–67, 1971–72 (also 1960–61 and 1973–74)
Establishment of refuges	Swans arrested	Welney 1968–69, Railway—Purl's Bridge 1969–70
Supplementary feeding	Swans arrested	Since 1971–72

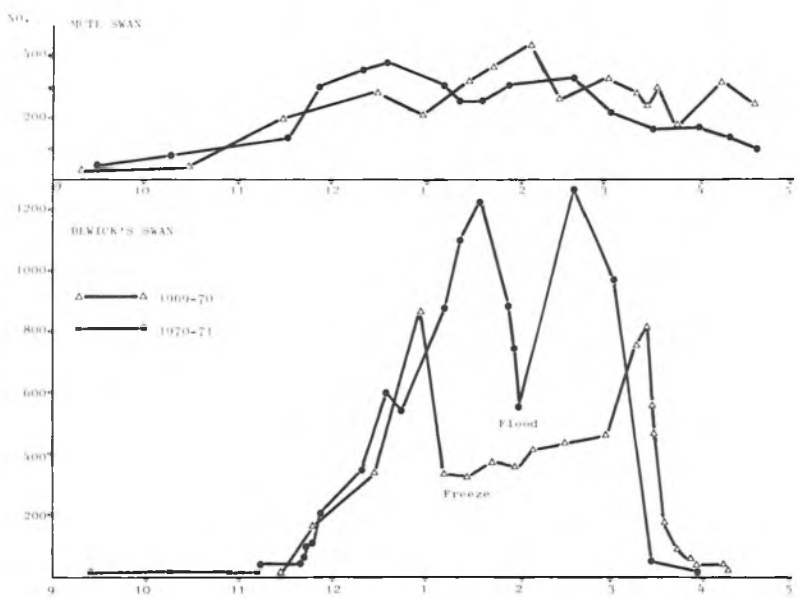

Figure 3. Mute and Bewick's Swan populations at the Ouse Washes, winters 1969–70 and 1970–71.

in the Netherlands and West Germany over the mild 1974–1975 winter, usage of the Ouse Washes by this species exceeded 80,000 swan days and was the fourth highest on record.

Bewick's Swans on other fenland washes and the Wash

In recent winters, when the Ouse Washes were deeply flooded, Bewick's Swans have moved up the River Ouse to meadows at Overcote (up to 200 birds), Swavesey Fen (up to 35), 4 km from the Ouse Washes, and as far as Fenstanton (up to 150), 10 km away (M. J. Allen and J. L. F. Parslow, pers. comm.).

The River Cam is largely embanked so that few fields still flood except near Upware, 13 km east of the nearest point on the Ouse Washes. When conditions were suitable the Cam washes were visited sporadically by small numbers of Bewick's Swans. The largest number recorded between the 1963 and 1974 winters was only 20.

The Nene Washes, 18 km north-east of the Ouse Washes, were flooded fairly regularly in winter until 1961–1962. Between 1952 and 1958 Bewick's Swans occurred every winter but the maximum was 18 (Cambridge Bird Club Reports). In the winters of 1958–1961, however, the maxima were 97, 44 and 180 respectively. Subsequently it became possible to control flooding on the Nene Washes to a great extent and many of the summer pastures were ploughed to the detriment of the swans. From 1961–1974 a few Bewick's Swans have visited the washes most winters but only when the Ouse Washes were deeply flooded, as in March 1969 and 1970 and in January 1971, has the population exceeded 30. The maximum number on these occasions has been 100.

Both the rivers Ouse and Nene flow into the Wash. The outfall of the Ouse is only 27 km from the north-east end of the Ouse Washes. In recent years most of the Bewick's Swans recorded on the Wash have been on the south and east shores, and they have occurred largely in the passage periods, October and November and again in March. The maximum recorded was 97 (BTO, RSPB, Wildfowl Trust Birds of Estuaries Enquiry).

Relationships between the Ouse Washes and Slimbridge populations of Bewick's Swans

Slimbridge on the Severn estuary lies only 200 km south-west of the Ouse Washes, yet there are reasons to believe that the two wintering populations are fairly discrete. First, there has been a corresponding increase in numbers and usage at both sites since 1955–1956 when Bewick's Swans began to visit Slimbridge each winter (Ogilvie, 1969). Secondly, whereas most of the swans leave Slimbridge before the end of February, large numbers frequently remain at the Ouse Washes until mid March. Though maximum numbers at the Ouse Washes have tended to occur in February there has been little evidence of an influx of swans coinciding with the main exodus from Slimbridge.

Thirdly, it has been possible to identify certain swans on the Welney Refuge which had previously visited Slimbridge by recognizing bill patterns and by reading the engraved numbers on plastic rings placed on them there (Evans, 1975; Ogilvie, 1973). In the 1970–1971, 1971–1972 and 1972–1973 winters some of the Slimbridge swans were marked with yellow picric dye as well as with rings. The identification of individuals in these ways has confirmed that there is some interchange of birds between the two populations but the number involved is relatively small.

Areas favoured by Bewick's Swans at the Ouse Washes and the effects of supplementary feeding and wildfowling on distribution

In the winters of 1969–1970 and 1970–1971 washes on either side of the Pymore railway viaduct and others in the Purl's Bridge–Welches Dam area were favoured during the first half of the winter when there was little flooding. By January the distribution was more scattered and deep flooding of the washes shifted the swans to the higher parts of the Ouse Washes at the south-west end, notably Sutton Gault, Berry Fen near Earith and Overcote (Figure 1). As the flood waters subsided in March the swans concentrated between Mepal and Welches Dam. The only large flocks on the Welney refuge were in January.

From the 1971–1972 winter, when supplementary feeding with grain started in the Welney area, it gained Bewick's Swans at the expense of other areas. This refuge held the majority of the Ouse Washes population during the 1972–1974 winters (Owen & Cadbury, 1975). The increased usage of this section over these two winters was significantly greater than in the 1969–1971 winters before supplementary feeding had started ($P < 0{\cdot}001$) with the 1971–1972 winter somewhat intermediate. Over the 1969–1971 winters

only 11% of the total usage by Bewick's Swans was of the Welmore-Welney section compared with 87% in the 1972–1974 winters. There is little doubt that the provision of a readily available source of food of high calorific value in an area free from disturbance had an important influence on this change. Transient swans which might have moved elsewhere, particularly if flooding conditions were unfavourable, were arrested. The creation of pools and of banks to prevent disturbance also contributed to the Welney Refuge's attractiveness to swans, especially in the winter of 1972–1973 when there was little flooding.

In the winter of 1970–1971, 60% of the usage of the Ouse Washes by Bewick's Swans during the wildfowling season (1st September–31st January) was within the two refuge areas. Later in the winter there was a movement out to utilize the other areas (Table 4). Usage of the refuge areas by this species was significantly greater before the end of January than subsequently ($P < 0{\cdot}001$). A similar trend was observed in the duck population (Thomas, in prep.). However, the difference was not significant ($0{\cdot}7 > P > 0{\cdot}6$) for Bewick's Swans in the winter of 1972–1973 when the habit of feeding on grain had become well established (Table 4).

Proportions of cygnets and brood size among Bewick's Swans

The proportion of cygnets at the Ouse Washes in each of the six winters 1969–1975 is given in Table 5. The average percentage for the December, January and February counts in each winter is taken for comparison with the proportion at Slimbridge (calculated from the total number of different individual swans observed during the winter). With the exception of the 1972–1973 winter the proportion of cygnets at the two sites was similar. In two winters there was a markedly lower proportion of cygnets among the swans at the Ouse Washes in November than in December. There was also a tendency for the proportion in February (average over 6 winters $13{\cdot}1 \pm 5{\cdot}4\%$) to be lower than in January ($15{\cdot}9 \pm 6{\cdot}8\%$). The difference is not significant but an influx of white-plumaged immatures or adults without families from elsewhere is indicated. The fact that the percentage of cygnets rose again in March suggests that the family parties tended to return to the Continent later.

Taking the national figures, there are six winters between 1954 and 1965 for which the proportion of cygnets is known in a sample of over 100 Bewick's Swans (Ogilvie, 1969). The mean proportion was $23{\cdot}8 \pm 9{\cdot}8\%$ compared with $14{\cdot}9 \pm 6{\cdot}5\%$ over the last eleven winters 1964–1975. Because of the wide variation, the difference between the means is not quite significant. Breeding success was relatively poor in three successive years, 1967, 1968, and 1969.

Average brood size at the Ouse Washes was calculated from the best single count in each of the six winters 1969–1975 (Table 6). The Slimbridge figures, which represent the average size of all broods observed each winter, correspond fairly closely with 1972–1973 again being an exception.

Table 4. Use of refuges at the Ouse Washes by swans.

	1970–71		1972–73	
	Total usage (swan days)	Usage of refuges (% of total)	Total usage (swan days)	Usage of refuges (% of total)
Bewick's Swan				
Wildfowling season	48,420	60	41,200	93
After 31 Jan	41,700	40	17,480	95
Mute Swan				
Wildfowling season	28,910	24	20,520	52
After 31 Jan	16,230	13	33,230	49

Table 5. Proportion of cygnets in the swan populations at the Ouse Washes.
Each set of monthly figures represents a single complete or near complete count.

		1969–70	1970–71	1971–72	1972–73	1973–74	1974–75
Bewick's Nov.	n	—	200	397	352	422	231
	%		8·3	8·8	16·2	25·6	9·5
Dec.	n	337	620	489	452	743	577
	%	6·2	18·1	10·6	14·8	23·6	18·8
Jan.	n	357	1234	914	626	1009	906
	%	6·7	22·4	10·6	14·2	24·3	17·2
Feb.	n	416	1278	1201	507	1053	871
	%	6·5	16·4	8·3	10·3	20·0	16·8
March	n	456	964	670	197	348	110
	%	6·4	19·4	10·3	18·3	22·4	16·3
Mean for months Dec.–Feb.	%	6·5	19·0	9·8	13·1	22·6	17·6
Slimbridge	%	7	18	11	19	24	20
Mute Jan.	n	363	310	308	210	224	311
	%	14·2	23·5	25·0	35·2	14·3	28·3
Whooper	n	32	28	27	22	31	53
No. of cygnets		6	7	7	1	16	19

Table 6. Brood sizes of Bewick's Swans at the Ouse Washes.
A single count taken for each winter.

		% of total broods				Mean brood size	
	n broods	1	2	3	4/5	Ouse Washes	Slimbridge
1969–70	19	(53	26	16	5)	1·7	1·6
1970–71	90	31	43	21	5	2·0	2·1
1971–72	54	55	30	15	—	1·8	1·7
1972–73	38	60	34	3	3	1·5	1·9
1973–74	81	30	23	30	17	2·4	2·1
1974–75	57	44	33	16	7	1·9	2·5

Mute Swan

The winter population of Mute Swans at the Ouse Washes

When censused in 1955–1956 the population of Mute Swans in England, Wales and Scotland was estimated as being between 17,850 and 19,250 (Rawcliffe, 1958; Campbell, 1960). The population was found to be similar in 1961 (Eltringham, 1963). The total in Ireland is considered to be in the order of 5,000–6,000 (Ogilvie, 1972). The average maximum number in January 1970–1975 at the Ouse Washes was 294 which represented 1·2% of the population in Britain and Ireland (Table 1).

The mean maximum in the ten winters, 1964–1975 (333 ± 71) was significantly higher than in six winters in the 1952–1964 period (237 ± 58). The highest number recorded on any date is 433 in February 1970. The mean usage of the Ouse Washes by Mute Swans over the winters 1969–1974 was higher than over the previous five but the difference was not significant (Table 2).

The south-west end (Earith and Berry Fen) remained an important area for Mute Swans at the Ouse Washes over the five winters, 1969–1974. Large numbers in this region occurred between mid January and late March, coinciding with flooding which apparently displaced birds from elsewhere on the washes. Swans from the Earith herd also used washes at Sutton Gault and during the deep flooding moved up the River Ouse to Overcote. By March the herd was largely composed of immatures, about 50% of which were cygnets.

Although the provision of grain at Welney did not have a marked effect on the usage of the south-west end of the Ouse Washes by Mute Swans, many birds which wintered in 1969–1971 in the Welches Dam–Purl's Bridge area and between Pymore railway viaduct and the Norfolk border apparently moved to the Welney refuge. Between 70 and 100 came to feed on grain between November and March in each of the winters 1971–1975 whereas previously few had used the Welney washes. In the 1970–1971 winter, usage by Mute Swans of the refuges compared with other areas was significantly greater in the wildfowling season than after the end of January ($P < 0{\cdot}001$). As with the Bewick's Swan, the difference was not significant ($0{\cdot}5 > P > 0{\cdot}3$) in the winter of 1972–1973 when supplementary feeding tended to retain birds on the Welney refuge.

The proportion of cygnets in the Mute Swan population at the Ouse Washes was higher in September and October, and again in the early spring than in winter. This trend appears to reflect a winter influx of white-plumaged but immature or non-breeding birds from other waters and their departure again in spring, leaving the first year birds and the local breeding population. Ringing results confirm the movement of swans from waters in the region to winter at the Ouse Washes. For comparisons of annual productivity, the proportion of cygnets in January is used (Table 5). Over the six winters 1969–1975 the average proportion of cygnets was 23·4% for the Mute Swan compared with 14·8% for the Bewick's.

The summer population of Mute Swans

In spite of the large numbers which winter in the area, the breeding population remained relatively small and fairly stable with 10–14 pairs over the five years, 1970–1974. In 1973, following a dry spring, there were only 10 breeding pairs compared with 14 in the previous two years when the washes were flooded in spring. More Mute Swans bred between Mepal and Purl's Bridge and between Welney and Welmore than in the other areas. The breeding population between Earith and Welches Dam averaged 4 pairs between 1970 and 1974. In 1697, shortly after the Ouse Washes were formed, 25 broods with 108 cygnets were 'upped' on this stretch (Ticehurst, 1957). Of the 38 nest sites recorded over the years 1970–1974, 19 were on dyke banks, 13 beside pools (an increasingly available habitat), five on river banks and one in an osier bed.

Non-breeding pairs, of which there were up to five, may have been immatures of two or three years old which would breed a year later (Minton, 1968). The herd of 60–70 immatures which gathered at Earith in the spring departed from the washes by early June. However, in two years before doing so these birds moved to the Purl's Bridge washes where there was a pool.

Relationships between populations of Mute Swans at the Ouse Washes and those elsewhere

There were six recoveries or controls of Mute Swans ringed at the Ouse Washes. Of the swans recovered or controlled at the Ouse Washes, 13 had been ringed at Cambridge and a further five elsewhere. The results allow some tentative conclusions to be drawn. The majority of Mutes using the Ouse Washes apparently remained within 32 km of the area. However, a bird ringed as an adult at the Ouse Washes in April was recovered in October of the same year at Hickling Broad (107 km NE) where it may have moulted.

The wintering population at the Ouse Washes included adults which summered at Cambridge, Littleport and locally. The immatures (first and second winters) included birds reared at Cambridge as well as locally. At least a proportion of the herd of immatures gathered at Earith in the spring moved to Cambridge to moult but the flock on the River Cam in the city has declined from 103 in 1964

to only 23 in 1971 (de L'Brooke, 1971). Other birds in the Earith herd, however, wintered at Cambridge. Some of the summering population of adults at the Ouse Washes wintered elsewhere in the region such as at Ely and Whittlesey.

Whooper Swans

Whooper Swans at the Ouse Washes

The great majority of the 4,500 Whooper Swans which winter in Britain and Ireland are considered to be from the population breeding in Iceland (Ogilvie, 1972). In November 1961, when a total of 3,107 were counted in Scotland, England and Wales, 17% were in the last two countries, largely in northern and western districts and none at the Ouse Washes (Boyd & Eltringham, 1962). However, the average maximum number at this site in January over the years 1970–1975 was 31. Though this number represented only 0·7% of the total population in Britain and Ireland (Table 1) the herd is the southernmost regular wintering one in England.

As with the two other species, the mean winter maximum over the 1964–1975 period (23·9 ± 14·0) was significantly higher than in 1952–1964 (8·2 ± 7·8). The highest recorded number is 80 in March, 1942 but 53 were present in January 1975. The mean usage of the Ouse Washes by Whooper Swans was significantly greater over the winters 1969–1974 than over the previous five (Table 2 and Figure 2).

In the 1969–1970 and 1970–1971 winters the relatively small population of Whooper Swans at the Ouse Washes was largely divided between two areas, at Welney washes and between Purl's Bridge and Welches Dam. Since the provision of grain, few have been observed outside the Welney area of the Ouse Washes. The usage of this section over the 1972–1974 winters was significantly greater ($P < 0{\cdot}001$) than that in 1969–1971 before supplementary feeding started.

While there was only a single cygnet among 22 Whooper Swans at the Ouse Washes in the 1972–1973 winter, the proportion exceeded 30% in the following two (Table 5). By contrast, in the 1974–1975 winter, the proportion of first winter birds in herds at most other sites in Britain and Ireland was much lower (M. A. Ogilvie, pers. comm.). This together with the fact that contaminated birds were present after an oil spill in the Netherlands in 1971 (Owen & Cadbury, 1975), provide limited evidence that Whooper Swans wintering at the Ouse Washes originate from Scandinavia or Russia, rather than from Iceland. The mean brood size at the Ouse Washes taking one good count each winter between 1969 and 1975 was 2·5 (15 broods). Boyd & Eltringham (1962) give a mean brood size of 2·7 for a sample of Whoopers in Britain which were largely if not all from the Icelandic breeding population. At the Ouse Washes in the 1974–1975 winter there was one brood of 6 cygnets, a number which is higher than any recorded in Iceland (M. A. Ogilvie, pers. comm.).

Relative numbers of the three species of swans at the Ouse Washes

These have been assessed by comparing the mean winter maxima of the three species over three periods: 1938–1952, before the 1952–1953 winter influx of Bewick's Swans (Nisbet, 1955), 1952–1964 and 1964–1975. In the first period, when coverage was incomplete in some years, the ratio of Whooper Swans to Bewick's was approximately equal (1:0·8). Since 1952 there has been a marked change with the overall ratio increasing to 1:33 in favour of the Bewick's Swan. Over the last two periods the relative numbers of the Mute Swan remained intermediate between that of the other two species, though the Whooper Swan increased in relation to the Mute (1952–1964, 1:21; 1964–1975, 1:13).

Discussion

While the International Wildfowl Counts from 1967–1973 indicated that the Bewick's Swan population wintering in north-west Europe was fairly stable over this period, they also showed that there has been a redistribution of birds. In the Netherlands, while numbers have risen on the IJsselmeer polders, meadows along the river Rhine and Waal and the Biesbosch have largely been forsaken by this species. In Britain and Ireland, increases have taken place at Slimbridge (up to 1971) and the Wexford Slobs, as well as the Ouse Washes (Atkinson-Willes, in press). It is unfortunate that recent information is lacking on the wintering population in Northern Ireland.

Nisbet (1955) drew attention to increasing numbers of Bewick's Swans wintering at the Ouse Washes and related this to a southward shift in the migration route between the Netherlands and Ireland so that they crossed England rather than Scotland. He suggested that the change may have been influenced by

the desalination of the IJsselmeer which encouraged more Bewick's Swans to stay in the Netherlands rather than move west to Ireland and the Outer Hebrides. On several occasions large numbers at the Ouse Washes can be related to the displacement of swans from the Continent as a result of cold weather, particularly if it did not extend to eastern England (Ogilvie, 1969). Such events may have played a part in establishing the Ouse Washes as alternative winter quarters to the Netherlands.

The usage of the Ouse Washes by Bewick's Swans has consistently exceeded 35,000 swan days each winter since 1965–1966, though it attained this level in only one previously. Certain features have made this wetland more favourable to the species. The absence of prolonged periods of freezing in the winters since 1969–1970 has enabled swans to remain in the area, though little flooding in 1972–1973 not unexpectedly reduced the attraction of the washes. The establishment at the Ouse Washes of refuge areas where there was permanent water and freedom from disturbance, encouraged the swans to stay and since the 1971–1972 winter they were further enticed by supplementary feeding.

Though usage of the Ouse Washes by Whooper Swans has increased, the population breeding in Scandinavia and western Russia, to which these birds at the Ouse Washes may belong, largely remains on the Continent, particularly the Baltic, even in cold winters. The movements of British Mute Swans are largely restricted to distances less than 48 km. Moreover, though the British population increased rapidly during the latter half of the 1950s, after a marked decline in the early 1960s, it has stabilized at a level which represents about 70% of the peak number (Ogilvie, 1967). Thus it is not surprising that the increase in usage at the Ouse Washes has been relatively minor compared with that of the Bewick's Swan.

There is no sign that the Ouse Washes has reached its maximum capacity to hold swans in winter other than in periods of very cold weather or deep flooding. Supplementary feeding and the recent behaviour of feeding on fenland farms (Owen & Cadbury, 1975) has largely removed even these limitations. However, the International Wildfowl Counts since 1967 (Atkinson-Willes, in press) have provided evidence that the population of Bewick's Swans wintering in north-west Europe is certainly no larger and has perhaps even declined since the 1955–1956 winter when up to 7,100 were counted (Nisbet, 1969). Considering the low productivity between 1964 and 1975 recruitment may have been insufficient to sustain this relatively small population. With areas of wet pasture land favoured by wintering Bewick's Swans diminishing on the Continent it becomes all the more important that optimal conditions are provided at the Ouse Washes.

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Summary

Since 1967 the Bewick's Swans *Cygnus columbianus bewickii* at the Ouse Washes have represented at least 14% of those wintering in North-west Europe and 45% of the population in Britain and Ireland. Maximum numbers have tended to increase and in three winters since 1969–1970 over 1,000 have occurred at one time. Between 1954 and 1974 there was more than a four-fold increase in the usage of the Ouse Washes by this species. The provision of supplementary food, starting in the 1971–1972 winter, together with freedom from disturbance resulted in a marked concentration of Bewick's Swans on the Welney refuge at the expense of other areas on the Ouse Washes which had previously been favoured. Deep flooding and freezing forced Bewick's Swans off the washes and passage birds were not attracted when there was little flooding. The population wintering at Slimbridge is relatively discrete from that at the Ouse Washes. Influxes were associated with severe winters on the Continent which displaced birds from the Netherlands. The mean proportion of cygnets over the winters 1964–1975 was only 15% compared with 24% in the 1953–1964 period. It is suggested that recruitment has been insufficient to maintain the Bewick's Swan population wintering in North-west Europe at its 1955–1956 level of at least 7,000.

The populations of Mute *C. olor* and Whooper Swans *C. cygnus cygnus* wintering at the Ouse Washes represent about 1% of their respective populations in Britain and Ireland. The herd of Whooper Swans is the southernmost regular wintering one in England and may originate from a Scandinavian or Russian breeding population rather than Iceland. Usage of the Ouse Washes by Whooper Swans has increased significantly in recent years. The distribution of both Mute and Whooper Swans of the area changed in response to supplementary feeding with grain on the Welney refuge. The relative numbers of Whooper Swans to Bewick's at the Ouse Washes have changed from approximate equality in the 1938–1952 period to 1:33 subsequently. On the other hand the number of Whooper Swans has increased in relation to Mute Swans since 1964.

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