The structure and behaviour of the Whooper Swan population wintering at Caerlaverock, Dumfries and Galloway, Scotland: an introductory study

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Introduction

The Whooper Swan *Cygnus c. cygnus* is a migratory species that breeds in Iceland, northern Scandinavia and the USSR. It is commonly believed that British wintering swans are predominantly of Icelandic origin (Boyd & Eltringham 1962; Atkinson-Willes 1981).

Earlier studies on Whooper Swans have been limited by the difficulties of identifying individuals in the field and by the absence of a regular ringing programme. Identification by natural markings, particularly individual differences in the black-and-yellow bill patterns, have been successfully used in studies of the Bewick's Swan *Cygnus columbianus bewickii* (P. Scott 1966). Whooper Swans also have individual bill patterns (Brazil 1981a), but the variations are less pronounced.

In recent years there has been a substantial increase in the number of Whooper Swans wintering at the Wildfowl Trust's Eastpark Wildfowl Refuge, Caerlaverock, in Dumfries and Galloway, Scotland. Encouraged by daily provision of grain many swans frequent the ponds in front of the observatories where they are studied at close quarters. A large proportion of the Caerlaverock flock has been ringed since 1979. This paper outlines the initial results of a study on population dynamics, feeding ecology and social behaviour.

Methods

The Caerlaverock National Nature Reserve, established in 1957, is situated on the northern shore of the Solway Firth and includes the whole of the Blackshaw Bank between the estuaries of the Nith and Lochar Rivers (Atkinson-Willes 1963). The Wildfowl Trust acquired the lease of Eastpark Farm in 1970 which includes some 243 hectares of merse (marsh) in the National Nature Reserve plus 95 hectares of arable fields and ponds. The number of Whooper Swans at Caerlaverock and at Islesteps, on the opposite side of the River Nith (Fig. 1), have been recorded by the mid-monthly National Wildfowl Counts since 1957-8. From 1970–1 the Caerlaverock data were augmented with daily observations by the Trust's refuge manager, C. R. G. Campbell.

In 1979 a swan trap was built at Eastpark Farm which is similar in design to the Slimbridge trap for Bewick's Swans (Evans 1982). From 1979-80 to 1983-4, 189 Whooper Swans (including 55 juveniles) trapped at Eastpark were weighed, sexed, measured, and ringed with large plastic (Darvic) and metal (B.T.O.) rings. The plastic rings were engraved with three-letter codes which could be read up to 300 metres with a telescope (Ogilvie 1972). Between the 1979-80 and 1982-3 seasons a number of swans were also marked with picric dye on their tail and wing tips to gather information about the migration routes when leaving Scotland. In 1983-4 a small spot of dye was put on the back of the head further to investigate local movements.

For the past five years the basic data which was collected for each ringed swan included age at first arrival, sex, parents and ringing details. Annual data included the arrival and departure dates for the swan, identity of mate, number of cygnets, and sightings outside the Caerlaverock area. Cygnets (first winter birds) were readily identified by their grey plumage, dull-coloured bill and their usual close association with parents. Whooper Swan yearlings (in their second winter) were generally more difficult to distinguish than Bewick's of the same age because many had developed full adult plumage without traces of grey plumage. However, a number of cygnets that were ringed and returned the following year substantiated the yearling class. Birds which were not paired and at least three years of age were classified as singles. Pairs were mated birds without young. A family contained at least one adult parent and one or more cygnets.

In 1983-4 daily attendance records were made for all swans ringed in previous years. Activities of the swans were recorded

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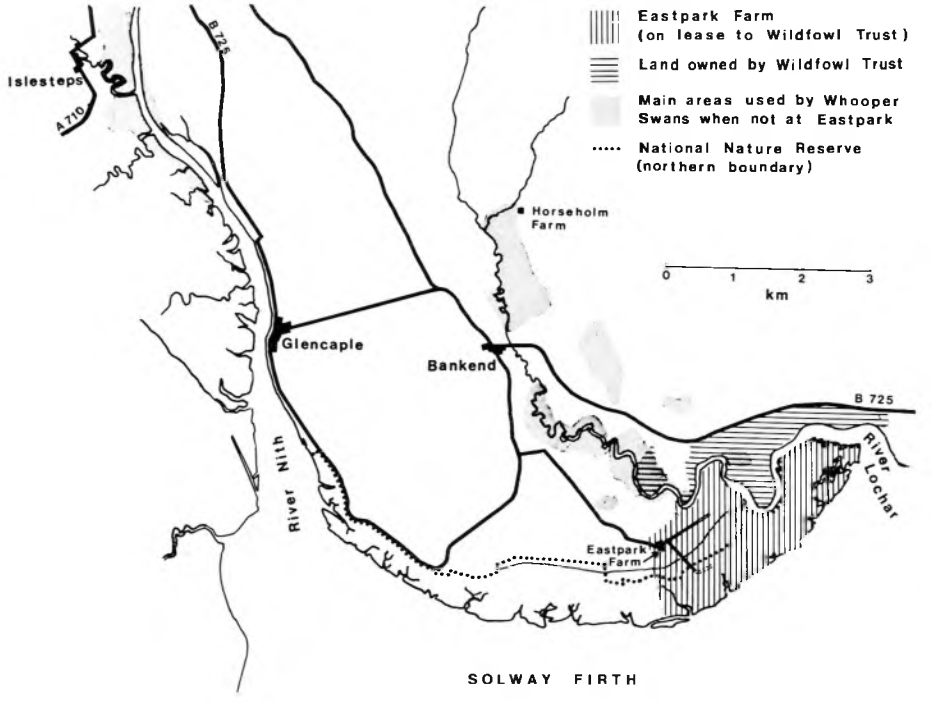

Figure 1. Caerlaverock and Islesteps habitats used by swans wintering at Eastpark Wildfowl Refuge.

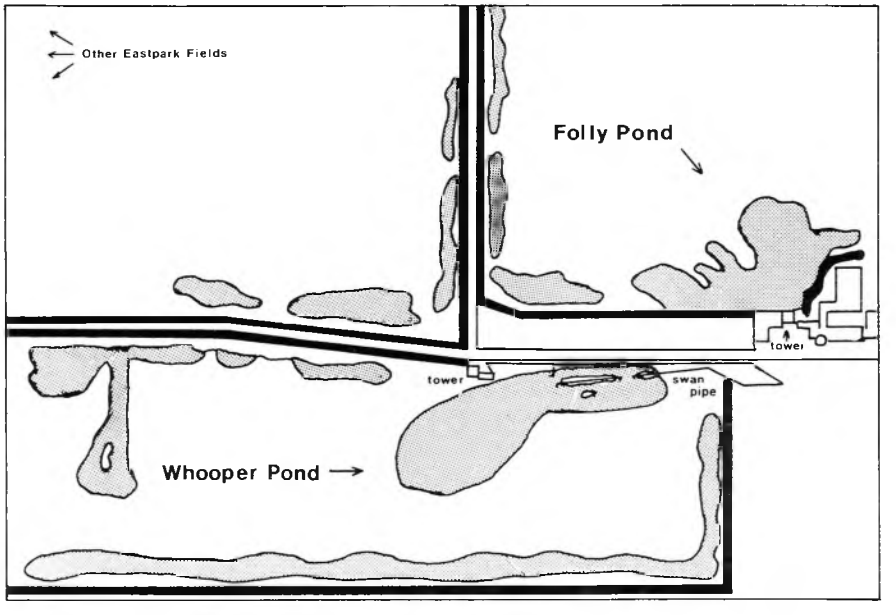

Figure 2. Layout of the Eastpark Wildfowl Refuge.

several times a day from a two-storey observatory tower (Fig. 2). An average of 5 'flock scan' observations were made for each hour of daylight for each month of the season (October–April). Eight continuous all day watches were made in which activities were recorded every 15 minutes. Activity observations included the number of swans present on each pond or field and the proportion of swans which were involved in feeding on water; grazing or digging on land; comfort activities (e.g. sleeping, sitting, preening and bathing); and loafing on water. Swans flying from the refuge to other Caerlaverock locations were counted and observed two or three times a week. From these sites faecal samples were collected for analysis (Owen 1975). In November, between 11.30 and 13.00 hrs, five minute continuous flock scans were made on swans which were feeding on different foods, including winter wheat, mixed grasses, barley stubble and potatoes. These were compared with observations made on the refuge. Density of the flock was determined by estimating distance between neighbours on a transect through the flock (D. K. Scott 1980a). Aggressive encounters, including all types of threats and contacts, were recorded during these scans.

Results

Build-up of the Caerlaverock population

Very few swans were reported at Caerlaverock up to the early 1970s although at Islesteps numbers increased from some 10 to 15 in the mid-1950s to a regular flock of 60-80 by the late 1960s (C. R. G. Campbell, pers. comm.). The development of the Caerlaverock population commenced in the mid-1970s and since the winter of 1975–6 the maximum number of swans has increased each year (Table 1). Indeed, the average maximum (124) for the seasons 1979-80 to 1983–4 now qualifies Caerlaverock as a site of international importance for Whooper Swans (D. A. Scott 1980).

The annual variation in percentage young at Eastpark ranges from 7.7% to 31.0% (overall mean, 17.5%) (Table 1), similar to estimates of breeding success in the total British Whooper Swan population between 1948 and 1961 (Boyd & Eltringham 1962). Breeding success for British Bewick's Swans over an 11-year span was 16.4% (Evans 1979a). However, since the two species have different breeding grounds annual variations in the two populations are assumed to be independent.

Recruitment to the Caerlaverock flock was not due to a relocation of the Islesteps population. The maximum number of swans at both sites increased simultaneously during the late 1970s. On the day of the peak Islesteps count in 1983-4, 85 on 23 March, there were 86 swans at Eastpark. The only other population in the southwest Scotland/northwest England area that has shown sustained growth in recent years is at Martin Mere, Lancashire, where numbers rose annually from 25 in 1980-1 to 117 in 1983-4. Martin Mere is also a Wildfowl Trust centre (established in 1975), so the build-up in

Table 1. Peak counts and percentage young of Whooper Swans at Caerlaverock and Islesteps from 1970 to 1984.

Season	Caerlaverock Maximum	Month	% Young	Islesteps Maximum	Month	% Young
1970–1	11	3 Nov	–	62	14 Feb	21.2
1971–2	3	12 Apr	–	65	12 Dec	30.8
1972–3	7	1 Mar	–	79	25 Feb	22.8
1973–4	15	24 Feb	26.7	73	17 Mar	–
1974–5	42	23 Feb	31.0	82	22 Nov	–
1975–6	26	21 Oct	7.7	90	13 Dec	–
1976–7	37	8 Jan	29.7	85	13 Mar	–
1977–8	59	13 Nov	13.6	115	22 Nov	13.0
1978–9	77	end Nov	11.7	153	10 Dec	13.7
1979–80	87	19 Dec	9.2	169	10 Dec	4.7
1980–1	91	27 Oct	17.6	119	18 Nov	17.7
1981–2	126	10 Dec	19.8	60	15 Dec	–
1982–3	150	15 Dec	16.0	142	12 Dec	–
1983–4	165	17 Nov	9.7	85	23 Mar	2.3

Whooper Swan numbers at both sites is probably related to the advantageous conditions created by the Trust. There is no evidence to suggest that the increase at Caerlaverock is due to a general southward shift (D. G. Salmon, pers. comm.).

Population structure

The structure of social classes among ringed Whooper Swans at Eastpark for the seasons 1980-1 to 1983-4 is given in Table 2. The proportion of swans with cygnets each year shows a negative correlation with the number of paired birds without young. But, on average, about one-third of all the paired birds returned with young. Singles from the largest group within the population show little annual variation, and probably include swans which were too young to breed. The proportion of yearlings is an underestimate in view of the difficulty in ageing by their plumage.

Distribution of sexes

Cloacal examination of the 129 adults caught has shown that the two sexes were equal (49.6% females). A slightly higher proportion of females (56.4%) recorded among 55 cygnets probably reflects greater difficulty in sexing at this age.

Return rates

The return rate of Whooper Swans to Eastpark proved very high with 78% of the ringed birds returning for at least one season. Furthermore, 40% of the swans originally ringed in 1979-80 returned for the four subsequent winters. As with Bewick's Swans (Evans 1979a; D. K. Scott 1980a) the highest return rate was among pairs (87.5% of 24) and families (85.7% of 7) while single adults (69.8% of 63) and yearlings (60.0% of 5) were less likely to return. The high proportion of cygnets that returned (78.6% of 42) was surprising compared with juvenile Bewick's Swans, which showed less attachment to their first wintering site. The return rate to Eastpark of males and females was not significantly different.

Of the 94 ringed adult Whooper Swans that returned to Eastpark six missed one winter. Two adult swans returned after missing two consecutive winters. Five yearlings and cygnets missed one season. Three were absent during the second winter after hatching (yearlings) and two during the third winter after hatching. All returned to Eastpark in 1983-4. Dispersal to other wintering grounds noted among young Bewick's Swans (Evans 1979a) thus to some extent also occurs with Whooper Swans. However, their eventual return reinforces the view that the population at Eastpark forms a stable winter flock.

Association with parents

Of the 84 cygnets identified with their parents, four were known to have disappeared during the winter and another brood of three was left at Eastpark after their parents departed. Of the four missing cygnets three belonged to the same pair; they lost two (out of four) in 1981–2 and one (out of four) in 1982–3. In 1983–4 a cygnet became separated from its original family (two parents and a brood of three) and joined a second family (a brood of three with a single female parent) in January. The cygnet joined the new family in triumph ceremony and aggressive activities, but was not allowed normal close proximity to family members (see D. K. Scott 1980b). Even though its original family was still present, the cygnet followed its new family from one pond to another and eventually they left the refuge together. The cygnet, however, failed to return to Eastpark with the family one week later.

Table 2. Proportions of ringed Whooper Swans in each class at Eastpark (percentage of total number).

Season	Families	Pairs	Singles	Yearlings	Cygnets	Unknown[1]	Total
1980–81	10.9	36.3	32.7	1.8	16.4	1.8	55
1981–82	20.4	17.2	28.0	9.7	22.6	2.2	93
1982–83	14.3	28.6	32.4	17.1	7.6	–	105
1983–84	11.5	36.1	36.1	5.7	10.7	–	122
Mean	14.4	29.3	32.5	9.3	13.6	0.8	93.8

[1] Denotes individuals which were not seen after ringing.

The brood size distribution of 84 cygnets with ringed parents varied between 1.9 and 3.4 (overall 2.6) throughout the study. For those 30 with unringed parents in 1982-3 and 1983-4 it varied between 2.4 and 3.6 (overall 3.0). The mean brood size was much higher than estimates made near Stirling (Brazil 1981a), but was similar to estimates for the total British population in the 1950s (Boyd & Eltringham 1962). The mean brood sizes given for both ringed (3.4) and unringed (3.6) parents at Eastpark in 1982-3 are higher than the largest mean brood size (2.74) noted in Iceland in October 1982 (Gardarsson & Skarphedinsson 1984). However, they report regional variation in the distribution of age ratios on the wintering grounds.

Pairing and breeding ages

Preliminary results on the age at which initial pair bonds are established were obtained by following cygnets and yearlings through to pairing. Two swans (one male and one female) were firmly paired in their second winter. Both retained their mates for at least two years (1982-83 and 1983-4). By the third winter (two years of age) seven out of 15 females were paired, compared to only one of seven males. These results are similar to those of Evans (1979b) for Bewick's Swans. Of 16 known-aged Whooper Swans seen with a mate, 14 (87.5%) were paired by their fourth winter (third year of age). In Bewick's Swans 73.8% are paired by then. Two female Whooper Swans did not mate until their fifth year. One then brought three offspring to Eastpark.

It is still too early to obtain meaningful results on the duration of pair bonds. However, it does seems that Whooper Swans keep the same mate for long periods. Of the five pairs ringed in 1979-80 four were still together in 1983-4.

Pair bonds were frequently established with swans from the same wintering site. In 24% of 33 occasions when ringed birds have returned to Eastpark with new mates both members of the pair had been at Eastpark simultaneously in the previous winter. In two of these cases one member of the pair had been paired to another mate. Whooper Swans have a higher level of courtship display activity on the wintering grounds in the spring months than do Bewick's Swans (D. K. Scott 1978).

Arrival and departure patterns

Whooper Swans have been present at Caerlaverock between late September and late April, although they usually arrived in numbers during the first half of October and departed in the second half of March (Fig. 3). The season of 1979-80 was considered separately because the harsh weather encouraged many Eastpark swans to move to Ireland in mid-winter. Less than 50% of the peak count that year remained after 1

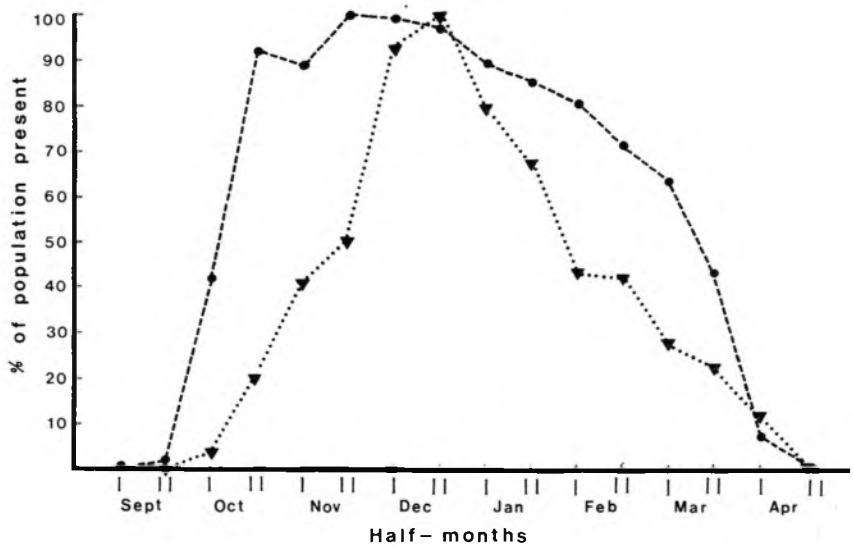

Figure 3. Number of Whooper Swans at Eastpark through the winter season. 1980–81 to 1983–84 (---); 1979–80 (...).

February. During the peak arrival period in October 89% of the 28 yearlings, 72% of the 29 families, 52% of the 60 singles and 51% of the 61 paired units had returned. This rapid return of ringed swans was expected because they were already familiar with the site. The arrival rate of yearlings was significantly greater than all other classes during October (Chi Square, $P<0.05$) and families returned faster than pairs and singles. There was no statistical difference (Chi Square) in the return rates between families, pairs and singles in November. A similar arrival pattern for Bewick's Swans at Welney, Norfolk, was recorded except that the main arrival period was one month later, in November (D. K. Scott 1980a).

The departure rate of the various social classes did not differ statistically during January, February and March. A slightly higher proportion of family units remained in the Caerlaverock area until April (10.3%). Shortly after arrival, 14.3% of the yearlings left (in October and November). Single swans were also more likely to leave soon after arrival. By the end of January, 28.3% of the single birds had departed compared to 17.2% of the families and 18.0% of the pairs.

Attendance levels

Analysis of the daily attendance records in 1983-4 supported the conclusion that single Whooper Swans were less attached to Eastpark than other classes. Single swans (21) spent more time away from Eastpark (37% of 91 days between arrival and departure) than 13 pairs with one member ringed (19% of 105 days), while 12 pairs with both birds ringed spent less time away (6% of 145 days). Eight families (9% of 134 days) and six yearlings (8% of 87 days) did not differ significantly from the latter.

During both 1982-3 and 1983-4, although families with experience of Eastpark were in attendance for most of the winter (mean number of days between arrival and departure 134), new unringed families stayed for only a few days. Six of the seven unringed families passed through in October and November, the other was seen in mid-March. Boyd and Eltringham (1962) found that the proportion of young Whooper Swans in Britain was lowest in mid-winter. This and the short-term stay in unringed families may be due to a movement to and from traditional Irish wintering grounds.

Sightings of Eastpark swans

One Whooper Swan was seen on the Tyne Estuary, Dunbar, East Lothian, 130 km NNE of Caerlaverock, three days before arriving there (Fig. 4).

There was only instance of a large proportion of the Eastpark swans moving to Ireland. Of the 50 swans that were caught and tail-dyed on 17 January 1980, seventeen were sighted in Ireland between 27 January and 17 February. Twelve were reported in a flock of 400 at Lough Swilly, Co. Donegal (27 January); a family of two adults and one cygnet were at Kilcoole, Co. Wicklow (between 6–17 February); two dyed adults were on the Roe Estuary, Co. Londonderry in a flock of 276 (in early February). All but five of the swans that were trapped had returned to Eastpark within two days of the catch (C. R. G. Campbell, pers. comm.). The stimulus for this movement is thought to be related to the harsh weather conditions that winter. Since 1979–80 there has been just one case of a ringed bird (with an unringed mate) returning to Eastpark during the autumn and then moving on to Ireland in mid-winter. A second Eastpark-ringed swan was seen at the same site, near Newcastle, Co. Wicklow, but had not been to Eastpark since the previous year. Two other Eastpark-ringed Whooper Swans in Ireland were reported in south Co. Kildare (late December 1980) and at Altore Loch, Co. Galway (in April 1982).

During the spring 25 swans have been reported in other parts of Scotland after leaving Eastpark. Ten of the sightings were of swans apparently following a NW/NNW route. Two swans were identified at Maybole, Ayrshire in March 1983; two dyed birds were at Gadloch, Strathclyde, Lanarkshire in late February 1980; one dyed bird was reported in the Outer Hebrides during late February and early March 1980, and a further five (a family with three cygnets) in March 1981. Ten dyed swans were reported near Hawick, Roxburgh, NE of Caerlaverock, in late February 1984. Five dyed swans have been sighted due north of Caerlaverock: one on the Insh Marshes, Inverness (March 1980); three near Thurso, Caithness (March 1980 and April 1981); and one at Sandwick in the Orkneys (April 1983).

The assumption that the British wintering population is mainly composed of Icelandic breeding birds is supported by several other

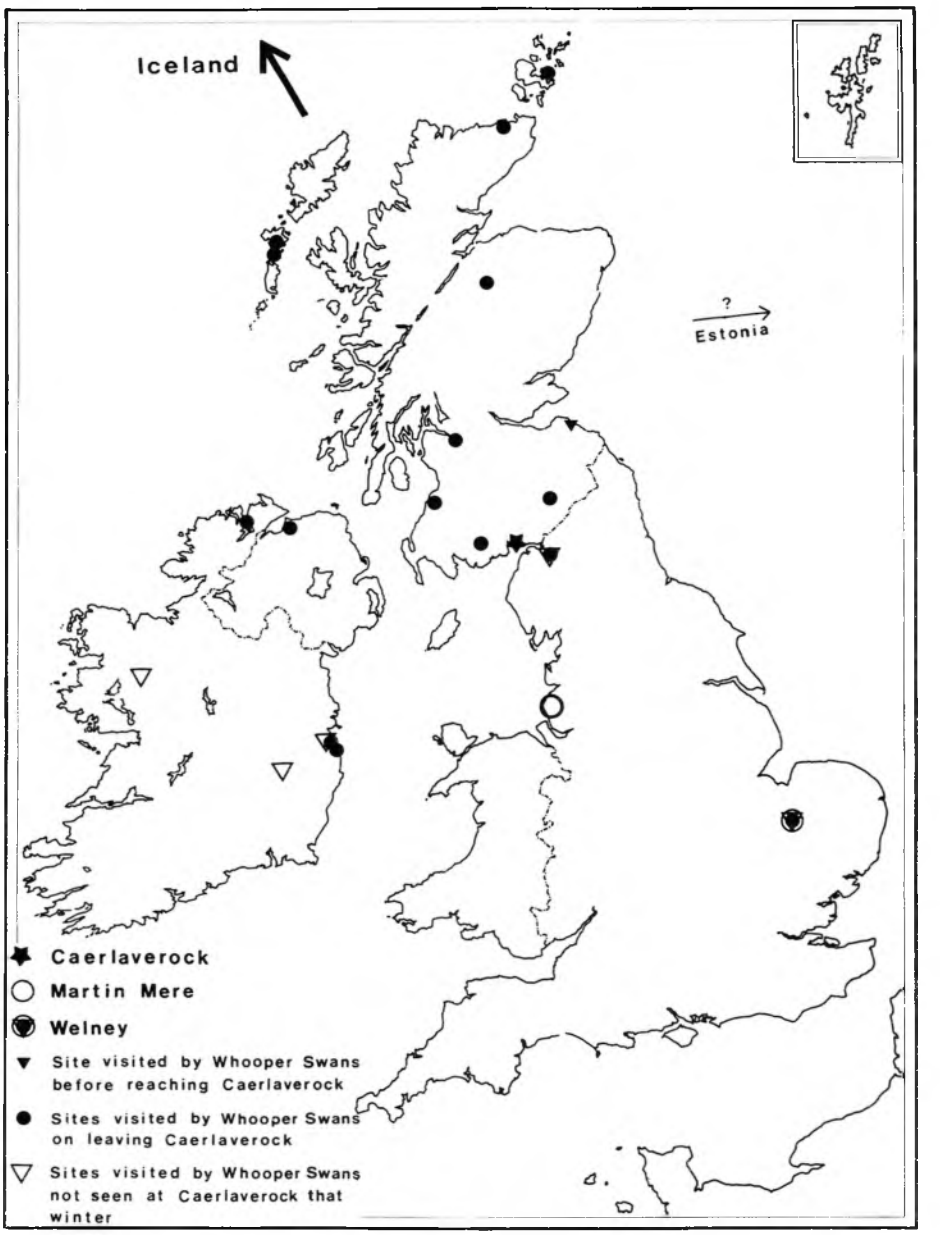

Figure 4. Resighting and recovery points of Eastpark-ringed Whooper Swans.

sightings. Seven ringed and dyed swans were reported in SE Iceland (during June 1980) and one moulted wing feather was found there (September 1980). Two yellow-tailed Whooper Swans were reported near Tallin, Estonia (April 1980), apparently heading for Siberian breeding grounds, but this sighting was not confirmed.

Ringed Whooper Swans are often reported in the autumn or spring at nearby sites. Twenty such individuals were identified at Islesteps between 1980-1 and 1983-4 after the birds had left Eastpark in the spring. After the dispersal of Eastpark swans in early March 1983-4, the number of birds at Islesteps was larger than at Eastpark for the remainder of the season. At this time six ringed birds were in the Islesteps flock. On

five different occasions ringed Whoopers have been sighted in mid-winter on the River Eden, near Carlisle, Cumbria, about 35 km ESE. At least eight marked Whooper Swans visited Loch Ken, 30-50 km west in February 1980. In all but two of these sightings the swans were also seen at Eastpark during the same season.

There was little interchange between the populations wintering at Eastpark and two other Wildfowl Trust reserves; Martin Mere in Lancashire, which has held up to 117 Whooper Swans and Welney in Norfolk with over 200. No ringed Whooper Swans have visited Martin Mere, but two reached Welney in 1982-3. One spent four days there before returning to Eastpark where it had been earlier that season. The second swan remained at Welney for the whole winter, but returned to Eastpark in the following October. Since 1980-1, twenty Whooper Swans have been ringed at Welney. One of these (ringed in 1982) visited Eastpark for one day in October 1983, arriving at Welney four days later.

Use of the refuge and surrounding area

The presence of absence of swans during the day in 1983-4 was closely related to three feeds provided at 09.00, 14.15, and 16.30. The peak number of birds usually ocurred after dusk when the last birds came into roost. About 15 birds left before the morning feed but the majority waited until the grain was depleted. A steady decrease in numbers continued throughout the morning until just prior to the 14.15 feed when numbers increased again and went on rising to the roosting total. The Bewick's Swans at Eastpark had a faster decline in numbers through the morning.

The birds that did leave the refuge made flights of 5 to 20 min to neighbouring farms. In 1983-4, destinations included 10 different farms, all of which bordered the Lochar River (Fig. 1). During that season 10 observations were made of Whooper and Bewick's Swans which either came from or went to Islesteps, usually in the morning. The numbers involved in the flights ranged between 2 and 25 birds (mean = 7.6, SE ±2.4). When ringed individuals in the Islesteps flock were identified with a telescope on 10 other occasions no more than six ringed birds were seen at any one time.

In December 1983–4 when the swans spent the most time away from the refuge the number which remained in the middle of the day dropped to fewer than 20 birds. Thus over 100 swans were feeding on neighbouring farms for about three hours a day. In contrast, there were several days in February when over 100 Whooper Swans were present on the refuge and there were absolutely no movements in or out. The strongest influence on daily departure patterns and refuge utilization appeared to be weather conditions, particularly temperature. On the coldest days swans tended to stay on the refuge.

Whooper Swans spent more time on the refuge than Bewick's Swans (Fig. 5). This difference was significant (Mann-Whitney U test: $U = 0$, $n1,n2 = 5$, $P = 0.008$, two-tailed). Bewick's Swans' relative unfamiliarity with the site could make them more wary. Only 41.7% of the 36 Bewick's Swans ringed at Eastpark between 1979-80 and 1982-3 have returned for a second winter. Another reason could be related to the fact that Bewick's Swans were dominated by the large Whooper Swans during aggressive encounters while feeding on the refuge, and may go elsewhere to graze.

In 1983–4, all Eastpark Whooper Swans roosted on refuge ponds throughout the season, whereas in 1982—3 they were also seen roosting on channels in the Solway Firth and on the ponds off the refuge.

Refuge habitat

Fig. 5 shows the average time that Whooper (64.4%) and Bewick's (45.8%) Swans spent on and off the refuge in 1983-4 and the amount of time they spent on different foods. The percentages were calculated from the total number of swan flocks sighted off the refuge (205 Whooper flocks and 89 Bewick's flocks).

The majority of time when on the refuge was spent on the main Whooper Pond, which is enclosed by a fox-proof fence, and where the first two feeds of the day are dispensed (Fig. 2). This enclosed area includes one large pond (1.5 hectares) and two long canal-like ponds around the perimeter of the pen. The long ponds were used extensively by swans mainly between the morning and afternoon feeds. Other birds which did not flight to non-refuge feeding areas in the afternoon made use of the Folly Pond and the associated borrow-pits along an embankment. This journey required a short 30-40 second flight over two

Figure 5. Habitats and main foods used in 1983–4 by a) Whooper Swans and b) Bewick's Swans. The outer circle shows the amount of time spent on the refuge and on other Caerlaverock areas. A = refuge ponds; B = refuge fields; C = recently planted grass; D = old grass; E = tubers; F = river vegetation; G = merse and ponds; H = barley stubble.

embankments and around other obstacles (buildings and the swan trap).

In the late afternoon the majority of birds flew over to the Folly Pond before the 16.30 feed and stayed there for the night. On moonlit nights the swans fed in the ponds and fields, but on darker nights they spent most of the night roosting on the water and banks of the ponds. At sunrise the birds usually fed from the borrow-pits and most early morning flights from the refuge left from there. All the remaining swans returned to the main Whooper Pond before the 09.00 feed.

At both of the locations swans made use of the fields as well as the ponds (Fig. 6), especially on the Folly Pond side where new grass was planted in the previous autumn. Whooper and Bewick's Swans spent different amounts of time through the day on the two main pond systems (Fig. 6). Bewick's tended to utilize the Folly Pond more than Whooper Swans at all periods of the day and throughout the season (Mann-Whitney U test: $U = 46$, $n1 = 12$, $n2 = 13$, $0.05 < P < 0.10$; $U = 0$, $n1,n2 = 5$, $P = 0.004$; two-tailed).

Activity budgets on the refuge

The main activities on the refuge were feeding and loafing on water, both about 30% of an average day. The remainder of the day was spent preening, sitting, sleeping, or bathing (lumped together as comfort behaviour, 22%), grazing or digging on land (about 8%) and extraneous behaviour including social activity (10%). The percentage of swans feeding obviously peaked at the times when grain was provided. The birds which finished feeding after 10.00 hrs began to engage in comfort behaviour (e.g. preening and sleeping). Then as comfort behaviour decreased loafing in water increased prior to the afternoon feed. The swans assembled in front of the observatory, where the food was dispensed, usually for more than an hour before the scheduled feed time.

These activities varied through the season (Fig. 7). The amount of time which was spent feeding peaked in February which was the coldest month in 1983-4. Grazing increased in March when the growth rate of the grass increased and comfort behaviour peaked both in October when the swans first arrived and in April when daylength was longest. The time spent loafing in water decreased through the season.

Interspecific competition: a comparison

By comparing daily feeding and comfort activities of all three swan species, including one all-day watch on 3 February when there were 132 Whooper Swans, 56 Bewick's Swans, and 50 Mute Swans *Cygnus olor* present (peak counts), it was found that Whooper and Bewick's Swans' peak feeding time was at the morning feed. Mute Swans fed earlier in the day, finishing off any grain which was still left over from the previous

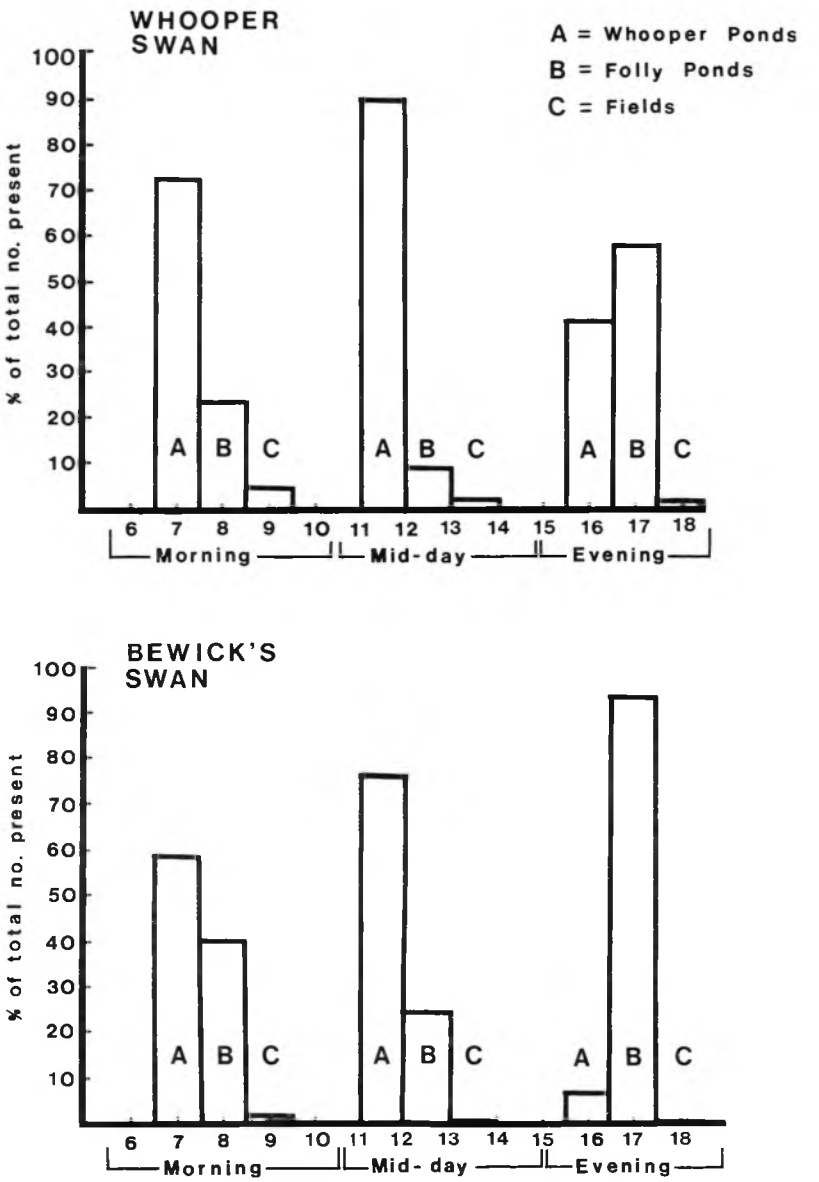

Figure 6. A comparison of the proportion of the day spent at different feeding stations by Whooper and Bewick's Swans. A = Whooper Pond system; B = Folly Pond system; C = grass fields (see Fig. 2).

evening feed, as the swans did not continue to feed close to the house after dark.

Less than half of the total number of Bewick's and Mute Swans on the refuge contested for feeding space when a majority of Whooper Swans were involved. The fact that Whooper Swans dominated both the other species might reflect the differences not only in the percentage feeding but also in the morning comfort activities. Many Bewick's and Mute Swans started these while nearly all the Whooper Swans were still involved in the feeding session.

The variations in behaviour between the three species is depicted in Fig. 8. The primary activity was different for each species which indicates their independence even sharing the same habitat with scheduled

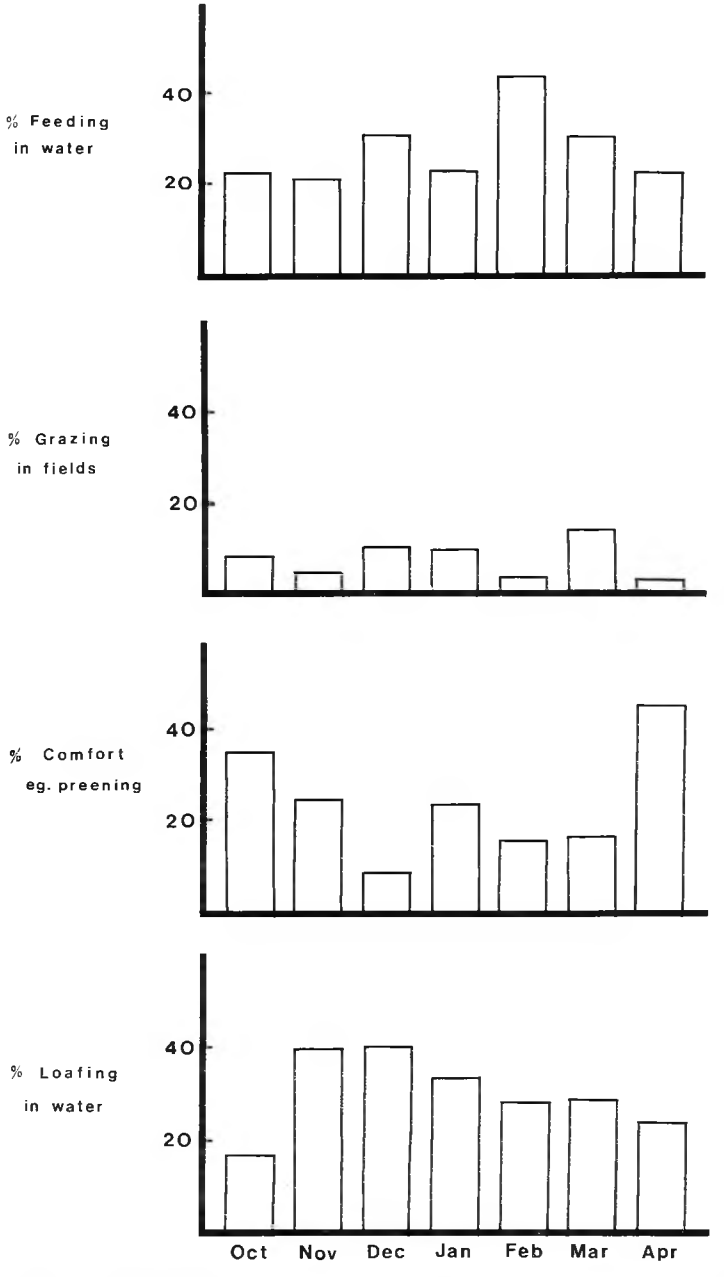

Figure 7. The activities of Whooper Swans in different months at Eastpark in 1983–4.

feeding periods. For Whooper Swans feeding was the most important activity. Comfort behaviour ranked third for Whoopers Swans, but first for Bewick's Swans. Mute Swans were again different in that their primary activity involved loafing or swimming on water.

Other Caerlaverock habitats

The time spent off the refuge and the foods taken varied during the winter. The timing of the different feeding regimes was determined by food availability. In October the swans fed on any barley which had been left

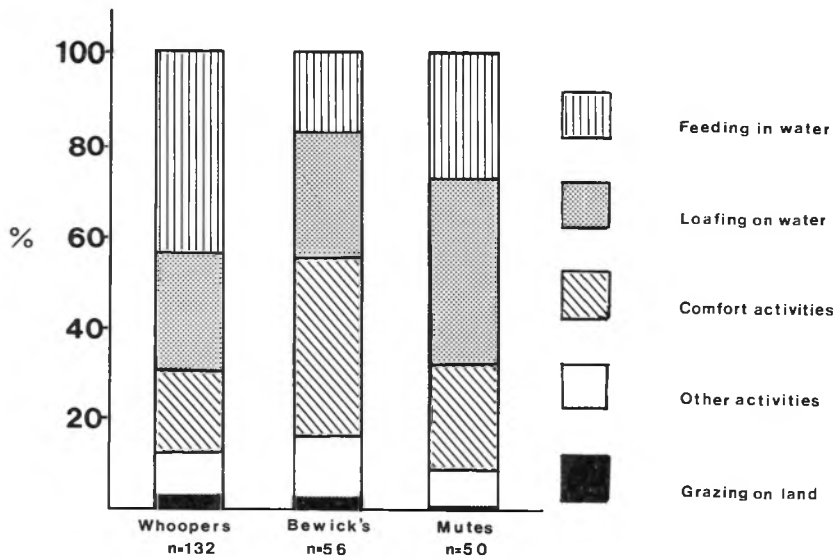

Figure 8. Comparison between Whooper, Bewick's and Mute Swans in the percentage of time spent on various activities at Eastpark.

over from the harvest. During the next month potatoes and turnips were harvested and again the swans exploited the left-overs. Also in November the swans began feeding on aquatic plants in the River Lochar, which was bordered by several fields of sprouting winter grass which they began to eat. In December a similar amount of time was spent on river plants and grasses. In January and February they spent 40% of the time on old grass and as the river began to freeze they increased the amount of time on new grass to about 50%. When this new grass began its spring growth in March and April the majority of time was spent there. Overall new grasses planted in autumn seemed to be the most important food for the Whooper Swans when off the refuge.

The largest concentration of swans throughout the 1983-4 season was on the refuge during the night roosting periods and during the morning feeds before very many birds left for other Caerlaverock areas. The largest flock (up to 106 birds) counted off the refuge were on the potato fields (mean = 35.4, SE ± 11.2, n = 10). The river and bordering fields attracted up to 105 birds (mean 58.7, SE ± 24.0, n = 16). Normally flocks in other Caerlaverock areas contained about 20 birds when off the refuge (Table 3) and even less when on grass fields away from the river.

The seasonal trends in feeding for Bewick's Swans were very similar to those of Whooper Swans except they did not exploit the new winter growth as extensively

Table 3. Flock sizes of swans in different habitats between October and March for Whooper Swans, and between November and February for Bewick's Swans in 1983–4.

Habitat	Mean	S.E.	No. of counts
Whooper Swans			
Eastpark (morning feed)	92.3	1.6	141
Other Caerlaverock fields	20.8	2.7	55
River	53.1	14.2	7
Islesteps	48.9	5.4	21
Bewick's Swans			
Eastpark (morning feed)	25.5	1.3	108
Other Caerlaverock fields	12.3	1.5	24
River	9.5	2.6	4
Islesteps	12.6	2.1	5

but fed on grasses which were planted in earlier years. This was probably due to direct competition with Whooper Swans on the same fields. On all habitats Bewick's Swan flocks were smaller (Table 3).

Species identification of foods

Analysis of several swan faeces was carried out to identify the species that were taken from various habitats in all months of the 1983-4 season. At Islesteps grass fields the swans fed almost entirely on *Lolium sp.* and secondarily on *Phleum sp., Alopecurus sp.* and little on other grass species. They also utilized merse areas near Islesteps where the main species which were taken included over 75% clover stolons *Trifolium repens* and some *Festuca sp.* and other merse grasses.

In the non-refuge Caerlaverock areas favoured grass species were again almost entirely *Lolium sp.*, and small quantities of other grasses.

Analysis of the faeces from waste crop fields confirmed that potatoes and turnips were taken. The development of feeding on waste crops by Whooper Swans is thoroughly discussed by Kear (1963).

The main plant content from droppings taken near the River Lochar included roots and tuber tissues and few leaves. The following river plants were collected *Callitriche sp., Myosotis scorpioides, Ranunculus sceleratus, and Sparganium emersum.* These findings support the casual observations that a large proportion of feeding time at the river was spent dipping under the water while the remainder of time was spent surface feeding, digging, and grazing from the side of the banks. The fact that droppings, collected in fields near the river, contained river plants indicates that there was frequent interchange between the fields and the river.

Fifteen droppings from Bewick's Swans were also collected. The same quantity and type of species were taken: mostly *Lolium sp.*, some *Phleum sp.* and little of other assorted grasses. Similar aquatic plant contents were identified in the Bewick's Swans' droppings taken from near the river.

Species which were identified from droppings collected at Eastpark, besides large quantities of barley, included primarily *Lolium sp.* and some *Phleum sp.*

Comparison of activities on and off the refuge

Flock scan data were collected in November (between 11.00–13.00 hrs) at Islesteps and compared with data collected in the same period on the refuge. The amount of time spent on comfort activities (41% and 44% respectively) were very similar in both locations. A further 45% of the day at Islesteps was spent grazing. Because of the relative ease of acquiring appropriate amounts of food for fulfilling energy requirements at Eastpark only a small amount of time was spent feeding in water (11%) and grazing (5%). This allowed 30% of the remaining time for swimming and loafing in water. However, birds spent more time (21%) on the refuge being vigilant (when feeding in grass fields) as compared with 13% for birds at Islesteps (Mann-Whitney U test for large samples: $z = 4.04$, $n1 = 21$, $n2 = 22$, $P < 0.00006$). This may be due to the greater human disturbance at Eastpark.

Comparing aggressive interactions on different foods

There was no difference in the frequency of aggression (threats and contacts) in the refuge and Islesteps flocks when the birds were grazing (Table 4). Aggression on the refuge pond was greatly influenced by the feed periods. During normal periods on the refuge ponds between scheduled feeding periods aggression was very similar to the level recorded on grass fields at Islesteps. When the swans assembled in front of the observatory before the grain was dispensed aggression increased and was highest after the grain was put out. These periods of intense interaction were short, lasting only as long as the grain supply, and even so did not exceed the level observed when feeding on barley stubble fields. A much lower level of aggression was observed on potato fields. The level of aggression in various situation was associated with density, but the differences were not significant.

Casual observation in late February and March indicated that aggression increased on both the refuge ponds and fields. This was caused by the development of an unusual behaviour which to our knowledge has never been documented in wildfowl. Whooper Swans were observed to have

Table 4. Comparison of aggressive interaction on and off the refuge when on different food types in November 1983.

Food	Number of observations	Aggression[1]	Number of swans	Estimated[2] density
Eastpark				
Grass	n=12	0.006	24.1	2.4
Pond between feeds	n=19	0.007	66.2	2.5
Pond prior to feeds	n=4	0.050	72.5	1.5
Pond during feeds	n=2	0.323	89.8	1.0
Non-refuge				
Grass	n=7	0.006	18.7	3.1
Potatoes and turnips	n=6	0.016	18.5	2.5
Barley stubble	n=3	0.576	24.3	2.1

[1] Measured as the number of aggressive threats and contacts per number of total swan minutes.
[2] Measured in swan lengths between neighbours on a transect through the flock.

aggressive confrontations over their own and their neighbour's faeces. Coprophagy in the Eastpark swans increased and became quite common by late March. Examination of these liquid faeces suggests that swans do not fully digest barley grain when eaten in large quantities without supplements of grass. It thus seems beneficial to make use of these faeces especially in the spring when individuals are building fat reserves. Conflict over these faeces was invoked by the act of defecating and by the posture of the bird which defecated; the bird often swung its head and neck around to look at the dropping. It was at this instant that neighbours approached and competition occurred.

Discussion

Eastpark Whooper Swans have clearly formed a traditional attachment to this wintering site, whereas the size and composition of a wintering Whooper Swan flock in central Scotland changed on a near daily basis (Brazil 1981b). At Eastpark 78% of the ringed swans returned for at least one winter mostly arriving in October and remaining until March. Only once was a large south-west movement to Ireland noted for Eastpark birds, during the hard winter of 1979-80.

Eastpark Wildfowl Refuge provides a unique environment for Whooper Swans to fulfil their daily and seasonal life cycle requirements and may enhance the process of reaching optimum breeding condition. The feeds provided and the readily available arable fields in the Caerlaverock area enable swans to obtain daily food requirements in less than half the time it takes for swans which do not use the refuge (e.g. Islesteps). This gives Eastpark swans extra time for other activities. The increased vigilance on the refuge may be related to increased disturbance, but not to an extent that is detrimental to the fulfilment of other activities. Otherwise the birds would not remain as loyal to the site. The time spent loafing on water may be the most beneficial difference between activities of refuge and non-refuge swans. D. K. Scott (1978) found that during loafing periods a large amount of pairbond activity occurred including triumph ceremonies which are assumed to strengthen the bond between paired birds (see Akesson & Raveling 1982). It is possible, therefore, that the pairs at Eastpark could have stronger bonds which would enhance their performance on the breeding grounds and ultimately their breeding success. At least 24% of swans that returned with new mates had paired to birds that wintered at Eastpark in the previous season. However, in Bewick's Swans wintering on a refuge there was no evidence that differences in pairbond "strength", and frequency of courtship display, were related to breeding success (D. K. Scott 1978).

In view of the large number of swans which utilize the other Wildfowl Trust reserves the carrying capacity of Eastpark and the surrounding Caerlaverock area seems far from limiting. This will probably result in an increasing number of swans that will make use of the waste crops, the Lochar River, and recent planted grass crops.

The extent to which swans damage agri-

cultural crops is minimal as stated by Owen & Cadbury (1975). At Caerlaverock the largest single concentration of swans feeding off the refuge was on potatoes which were left over from the harvest and not of economic importance. Flocks which exploited newly planted winter grass fields away from the river were small in number. Most swans leave the area before the peak spring growth, which further minimises the effect on crops. One possible conflict is foreseen involving new grass crops planted in fields bordering the River Lochar, where large concentrations of swans occur in autumn. However, from direct observation of the swans feeding on sprouting grass and from faecal analysis there is no evidence that seeds are dug up or that any other part of the plants are taken except the leaves, thus the roots remain intact.

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Summary

Since the mid-1970s there has been an annual increase in the number of Whooper Swans *Cygnus cygnus* wintering on the Eastpark Wildfowl Refuge, Caerlaverock, Dumfries and Galloway, Scotland, which is now a site of international importance for the species. Between 1979–80 and 1983–4, 189 Whooper Swans were marked with leg rings at Eastpark. Overall, 78% of the ring swans returned to Eastpark for at least one winter and 40% of the swans which were ringed in 1979–80 returned for four successive years. Swans first identified as pairs or families were more likely to return than singles and yearlings. There was no significant difference in the return rates of male and female swans.

The population contained an equal distribution of the two sexes. Singles formed the largest social class (32.5%) and showed little annual variation. The proportion of swans with cygnets fluctuated, but on average about 30% of the known pairs brought young. Mean brood size ranged from 2.0 (1983–4) to 3.5 (1982–3).

Females paired earlier than males. Only one known-aged swan (five-year-old female) has returned to the wintering grounds with offspring. Two swans (one male and one female) were firmly paired at one year old (second winter). Mates are frequently chosen from the wintering flock.

The main arrival period at Eastpark was during October and most swans departed in March. Yearlings arrived first, followed by families, then by pairs and singles. There was no significant difference in the departure patterns of the different classes. Single swans spent a higher proportion of time away from the reserve than other classes.

Sighting data support the view that Whooper Swans wintering at Eastpark are from Icelandic breeding grounds and that the Caerlaverock area is usually the final wintering destination for most of these birds, rather than a staging site during migration to Ireland.

Whooper Swans spent the majority of the winter season on the Eastpark Refuge but also made use of the surrounding arable land especially in the autumn and spring. Bewick's Swans *Cygnus columbianus bewickii* made significantly less use of the refuge. In October, Whooper Swans fed mainly on barley stubble and old grasses, moving to potatoes and aquatic river plants in November and December. Newly-planted winter grass was favoured by the swans from February until they left the area in late March and April. Grass species were identified from droppings.

Activity budgets showed that Whooper swans spent most time on the refuge feeding and loafing on water (both 30%) and the remainder of the day was spent in comfort behaviour (22%) and grazing (8%). A comparison of activity budgets and their seasonal variations was made with Bewick's and Mute Swans *Cygnus olor*. Observations on the Whooper Swans at Islesteps (11 km NW of Eastpark) indicate that a much higher proportion of the day was spent grazing (45%) than at Eastpark (16% combined grazing and feeding in water), and suggestions are made that Eastpark swans may benefit from the longer periods of loafing on water. There was no difference in the frequency of aggression between the refuge and Islesteps, although intense periods of interaction occurred at Eastpark after the grain was put out. Aggression increased on the refuge during spring because of coprophagy on faeces which contained large amounts of undigested barley.

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