Fifty years of swan research and conservation by The Wildfowl & Wetlands Trust

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The Wildfowl & Wetlands Trust (WWT) has contributed to the conservation of swan species by establishing refuges for the birds in winter, through its research programmes, and by advising others on site management. This paper describes an increase in the number of migratory swans wintering at Slimbridge, Caerlaverock, the Ouse Washes and Martin Mere following the development of WWT Centres at these sites. The build-up in numbers may be due to changing population levels, and to conditions created by WWT. We describe changes in feeding site selection in the last 50 years, and consider the potential for inter-specific competition between Bewick's and Whooper Swans in areas where the two species co-exist. WWT's long-term studies of individual birds, which have provided detailed insight into the swans' life-cycles, are reviewed. The importance of international collaboration for the effective conservation of migratory waterbirds is again emphasised.

The Wildfowl & Wetlands Trust (WWT) has a well established reputation for swan research, starting with census work during the 1950s (e.g. Boyd & Eltringham 1962; Ogilvie 1969), developed through the detailed study of Bewick's Swans *Cygnus columbianus bewickii* wintering at Slimbridge from 1964 onwards, and now including a long-term study of Whooper Swans *Cygnus cygnus* in both Britain and Iceland. Since the migratory Bewick's and Whooper Swans traverse political boundaries, international collaboration has been an important part of the studies, with fieldwork extending to the swans' migratory sites and breeding grounds in recent years. Studies of the resident Mute Swan *Cygnus olor* have been less intensive; the more sedentary nature of this species lent itself to regional population studies being undertaken in different parts of Britain. Nevertheless, WWT helps with the detailed study of the breeding colony of Mute Swans at Abbotsbury in Dorset, acts as a clearing-house for colour-ring sightings of Mute Swans, and periodically co-ordinates special surveys to assess its status and distribution within Britain (e.g. Boyd & Ogilvie 1964; Ogilvie 1967; 1981; 1986; Delany *et al.* 1992; Kirby *et al.* 1994; Rees *et al.* in press).

The basis for both the Bewick's and Whooper Swan research programmes is to monitor the life-histories of individual birds, in order to determine factors affecting their survival and life-time reproductive success. These may be used to explain changes in population size and distribution, and to identify their ecological requirements, which in turn help towards the conservation of the species. Comparative studies have described the different constraints on the swans' migratory and reproductive cycles, due to Bewick's Swans having a 2,500 mile (4,000 km) migration to breed in arctic Russia, whereas British-wintering Whooper Swans have a shorter 500 mile (800 km) flight to their Icelandic nest sites (Rees *et al.* 1996). Results of the studies have been disseminated through the publication of numerous scientific papers and theses, some purely academic, but mostly of an applied nature. Information gained on the swans' natural history has also been disseminated through WWT's education programmes, through interest taken in the studies by the media, through the Swan Supporter Scheme, and through advice given on the management of sites for swans.

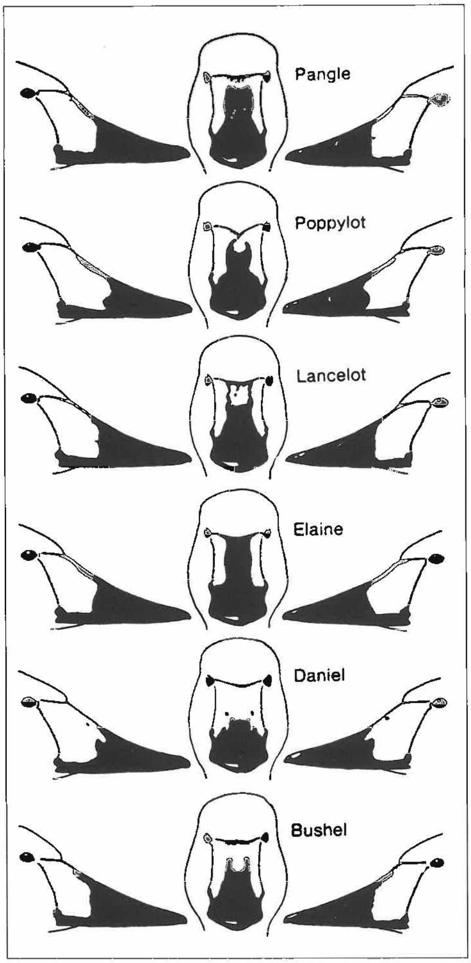
The Wildfowl & Wetlands Trust also contributes to the conservation of migratory swans through its network of refuges across Britain. Four WWT Centres now receive internationally important numbers of swans: Slimbridge, Gloucestershire (mainly Bewick's Swans); Caerlaverock, Dumfriesshire (mainly Whooper Swans); Martin Mere, Lancashire (both species) and Welney, Norfolk (both species). Arundel in Sussex provides a valuable cold weather roost site for Bewick's Swans wintering at Pulborough and Amberley in the Arun valley. In this paper we review the history of swans and the WWT, describe how their numbers and distribution have changed following the development of new Centres, and highlight the main results of the research programme.

History of Bewick's Swans in the Gloucestershire area

When the Wildfowl & Wetlands Trust (then known as the Severn Wildfowl Trust) was founded at the New Grounds, Slimbridge, in 1946, only small numbers of Bewick's Swans occurred in Gloucestershire – during the 1950s there were never more than 30 individuals counted on a single day (Ogilvie 1969). Those at Slimbridge were usually seen on the "Dumbles", 65 ha of raised saltmarsh between the sea wall and the Severn estuary which occasionally floods during high tide. In February 1964, 24 out of the 32 wild Bewick's Swans, then at the New Grounds, were attracted to the Rushy Pen within the WWT's enclosures by the presence of seven captive members of the same species, and continued to visit the pen for the remainder of the winter (Scott 1966). Sir Peter Scott and his family, watching the swans from their studio window, realised that individual birds could be identified by variations in their black and yellow bill markings (**Figure 1**), and this finding has formed the basis for the long-term study of the species. They also found that Bewick's Swans have a high level of winter site fidelity, with the same individuals returning to Slimbridge over several years, and that paired birds generally remain with their mates and offspring throughout the winter. Thus, it was possible to gather information on the swans' lifetime pairing and breeding success without relying on artificial markings. The number of swans at the New Grounds rose annually until 1970-71, when 627 individuals were identified by bill pattern during the season and 411 were present on one day (Evans 1979a, **Figure 2**). The period of recruitment to the Slimbridge flock appeared to reach a plateau in 1969-70, since the proportion of "experienced" swan units (i.e. where the individual, or at least one member of a pair or family, had been recorded at Slimbridge in a previous winter) exceeded the proportion of new swan units from the 1969-70 season onwards (Evans 1979a; Rees 1988; Bowler 1996).

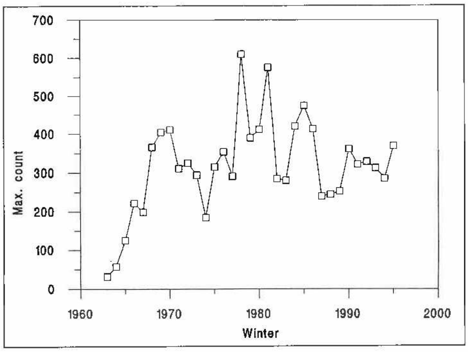
Regular records of the distribution of Bewick's Swans wintering in Gloucestershire since 1951 show that Bewick's Swans frequent only a limited number of sites in the area. The Gloucestershire Bird Reports record just 13 main sites as being visited by swans in more than one winter, with incidental sightings at a further 26. The major sites were the New Grounds, the Slimbridge Moors, Frampton Gravel Pits, Awre, Arlingham, Rodley, Walmore Common, Elmore Back, Ashleworth and Hasfield Hams, Coombe Hill Canal, the Avon Meadows, the Cotswold Water Park and Aylburton Warth to Lydney New Grounds. All are closely associated with the River Severn, or its tributary the River Avon, except for the Cotswold Water Park which is separated from the Severn estuary by the Cotswold Hills. Ring resightings indicate that, although the birds may move readily between sites along the River Severn, the small numbers seen at the Cotswold Water Park do not seem to

Figure 1. Individual differences in bill patterns in Bewick's Swans. Illustration by Dafila Scott, from Scott (1988).



be from the same flock as those wintering on the Severn (Rees 1988, 1990). A comparison of the maximum swan counts obtained at the New Grounds each winter with the population trend indices for Gloucestershire (calculated using the methods described in Owen *et al.* (1986), which control for changes in the number of sites surveyed from year to year) found that the increase in numbers at the New Grounds was positively correlated with the numbers recorded throughout the county (Rees 1988). It seems, therefore, that the development of the Slimbridge-

Figure 2. Maximum number of Bewick's Swans counted at Slimbridge each winter (1963-64 to 1995-96 winters inclusive).

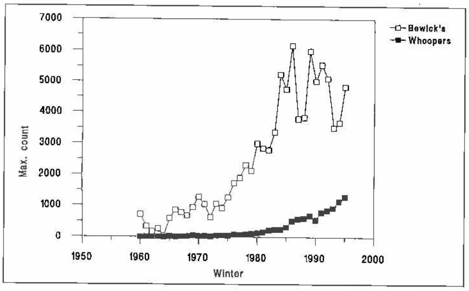


wintering flock resulted in more swans using other sites in the surrounding area, rather than Slimbridge acting as a "sink" by attracting birds from nearby sites. Moreover, sightings of ringed individuals indicate that some swans move out of Gloucestershire during the winter, and up the River Wye, to use a range of floodplain sites in adjacent Herefordshire.

Within Gloucestershire, the swans still frequent most of the sites used in the early years, together with a new site during the 1995-96 winter at Minsterworth Ham. Indeed, the numbers seen at Walmore Common resulted in its being designated by the British government as a site of international importance for the species under the Ramsar Convention in 1991. Walmore Common, like Rodley and the water meadows around the old Coombe Hill canal, is a low-lying pasture encircled by higher ground which floods during periods of heavy rainfall. Normally the water basins drain through a system of ditches into the River Severn but, if the river is high and the water is unable to escape, flooding may persist for several weeks, at which time the fields are used by large numbers of swans. The Slimbridge Moors is similarly an area of wet fields, dependent upon gravity drainage through the rhines. Elmore Marsh and Ashleworth/Hasfield Hams lie adjacent to the Severn and are subject to flooding if the river is in full spate; the meadows along the River Avon north of Tewkesbury are similarly vulnerable. Elmore provided an important shooting marsh during the mid 1950s but was drained in the early 1960s and has not been used by substantial numbers of waterfowl since then. The Gloucestershire Naturalist Trust purchased Ashleworth Ham in 1968, since when it has been managed as a nature reserve, and the deliberate retention of water by closing the sluices in winter has resulted in Bewick's Swans using it as an alternative roost site. At the New Grounds, the swans still feed on the "Dumbles" saltmarsh, but now more usually feed on improved pasture or occasionally on arable land. Aylburton Warth provides the only other section of raised saltmarsh in the area; again the Bewick's Swans occur not only at Aylburton Warth but on the reclaimed Lydney New Grounds beyond.

Originally it was assumed that the build-up in the number of Bewick's Swans wintering at Slimbridge was due to the conditions created by WWT, with the regular provision of grain in the Rushy Pen and protection from disturbance on the refuge encouraging the birds to return to the area. The population was then augmented by birds familiar with the New Grounds bringing their new mates and offspring to the site. Whilst these factors are likely to have reinforced the New Grounds as a regular wintering site for the birds, other studies have indicated that there has been a substantial increase in the number of Bewick's Swans wintering throughout northwest Europe since the 1960s. Some 6-7,000 swans were recorded in the early 1970s (Atkinson-Willes 1976), up to 10,000 in the mid 1970s (Atkinson-Willes 1981), 12,000 by the late 1970s (D.A. Scott 1980) and 16,500 during the winter of 1983-84 (Beekman *et al.* 1985), whereupon numbers stabilised with some 16-17,000 in the late 1980s (Dirksen & Beekman 1991; Rose & Scott 1994). It has been suggested that the earlier surveys underestimated the size of the total population (Beekman *et al.* 1985), but regular observations at the Ouse Washes, the main wintering site for Bewick's Swans in Britain, reinforced the view that there was a genuine increase in the number wintering in Britain during this period (Owen *et al.* 1986, **Figure 3**). There may also have been a movement of birds from The Netherlands to Britain during the 1960s due to the decline in submerged aquatic vegetation in the Ijsselmeer, which was an important food supply for the birds during the 1950s (Poorter 1991).

Figure 3. Maximum number of Bewick's and Whooper Swans counted at the Ouse Washes each winter (1960-61 to 1995-96 winters inclusive).



Build-up in numbers at other WWT Centres

Although the increase in the number of migratory swans wintering at the New Grounds could be due to changing population levels, there was a similar increase in flock size following the development of WWT Centres at Caerlaverock in 1970 (**Figure 4**), and at Martin Mere in 1975 (**Figure 5**). The Ouse Washes was already an internationally important site for Bewick's Swans when the WWT Centre at Welney opened on the northern end of the Ouse Washes in 1970, and it was one of the sites designated when the UK joined the Ramsar Convention in 1976, but numbers have since continued to rise (**Figure 3**). The peak count of 6,164 Bewick's Swans on the Ouse Washes in January 1987 represented one third of the northwest European population, then estimated at 16,500 birds. Whooper Swans tend to occur in smaller groups than Bewick's Swans and are more widely dispersed within Britain (Kirby *et al.* 1992). The maximum counts made on WWT reserves during the 1994-95 season (a total of 1,838 birds) together

Figure 4. Maximum number of Whooper Swans counted at Caerlaverock each winter (1970-71 to 1995-96 winters inclusive).

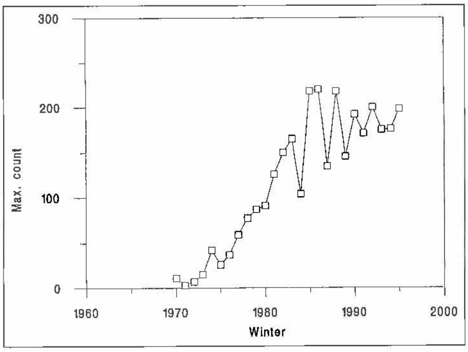
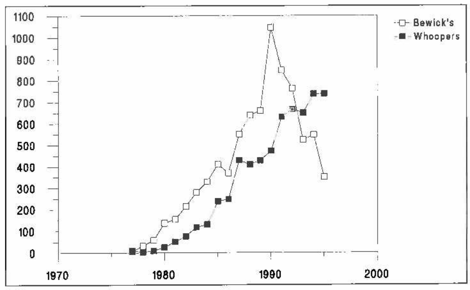


Figure 5. Maximum number of Bewick's and Whooper Swans counted at Martin Mere each winter (1977-78 to 1995-96 winters inclusive).



accounted for only 12% of Whooper Swans wintering in Britain, Ireland and Iceland.

Very few Whooper Swans were reported at Caerlaverock up to the early 1970s, despite the creation of the Caerlaverock National Nature Reserve on the northern shore of the Solway in 1957. Islesteps on the opposite side of the River Nith received some ten to 15 birds in the mid-1950s and there was a regular flock of 60-80 individuals by the late 1960s. Recruitment to the Caerlaverock flock was not due simply to relocation from Islesteps; numbers at both sites increased during the late 1970s and 1980s, and observations of ringed birds indicated that individuals used both Caerlaverock and Islesteps during the winter (Black & Rees 1984). The only other migratory swan population in southwest Scotland and northwest England to show such sustained growth at this time was at Martin Mere (**Figure 5**), reinforcing the view that the birds were attracted by the conditions provided by WWT. There is some evidence for an increase in the Whooper Swan population during the 1960s and 1970s, which might account for the initial influx to Caerlaverock and Martin Mere, with estimates ranging from 4,000 in Britain in November 1960 (Boyd & Eltingham 1962) to around 14,000 in the Icelandic breeding population by 1984 and 1985 (Gardarsson & Skarphedinsson 1984; 1985). Co-ordinated censuses of 16,700 in January 1986 (Salmon & Black 1986), 18,035 in January 1991 (Kirby *et al.* 1992) and 15,842 in January 1995 (Cranswick *et al.* 1996), show only limited population growth thereafter, indicating that the continued increase in numbers at Martin Mere during the 1990s may reflect a redistribution of Whooper Swans wintering in Britain. Interestingly, Whooper Swan counts at Caerlaverock stabilised at around 200, whereas at Martin Mere they have recently reached 700. The development of the Whooper Swan flock at the Ouse Washes is comparatively recent, perhaps because this is towards the southernmost end of their range. Here too numbers are still increasing, and this now constitutes the largest wintering herd in Britain. Welney and Martin Mere are both in areas of Grade A1 arable land, whereas Bewick's Swans at Slimbridge and Whooper Swans at Caerlaverock feed on the grasslands prevalent in these areas. The provision of a secure roost (in the form of large lakes with shallow edges, which are protected from disturbance), in areas with a super-abundant food supply of root crops and winter cereals, is almost certainly the reason for migratory swans concentrating at Martin Mere and the Ouse Washes.

Changes in feeding site selection

During the early part of this century the migratory swans fed mainly on aquatic vegetation in winter, particularly on

Zostera and *Chara* species in shallow coastal areas and on the tubers and root stalks of *Potomageton* species in freshwater lakes and marshes (Poorter 1991; Owen *et al.* 1986). Drainage and eutrophication have resulted in a decline in traditional winter habitats, which together with the shift towards arable cultivation has resulted in the swans switching to feed on arable land and improved pasture over the last 30 years. Whooper Swans were reported on potato fields during severe weather conditions during the 1940s, but this did not become a regular habit until the 1960s (Kear 1963; Pilcher & Kear 1966; Merne 1972; Sheppard 1982). Kear (1963) implied that the tendency to feed on potatoes followed a change in the distribution of Whooper Swans during the twentieth century, with more birds wintering in central Scotland, an important area for arable farming. It is not clear, however, whether the change in distribution was led by Whooper Swans actively selecting arable sites, rather than a reduction in traditional feeding sites elsewhere. The tendency for Bewick's Swans to feed on arable land did not become established until the 1970s. The first record of Bewick's Swans grazing on winter wheat was with Whooper Swans in Roxburghshire in 1968 (MacMillan 1969), and they are known to have been feeding on root crops by 1972 (Merne 1972; Owen & Cadbury 1975). Since 1972-73, Bewick's Swans wintering on the Ouse Washes have switched from a diet of soft grasses, found on the semi-natural wet grassland of the Washes themselves, to spend more time feeding on waste crops of potatoes and sugar beet, and also on cereals, in the nearby fields (Owen & Cadbury 1975). Moreover, the swans on the Ouse Washes are still using arable land 20 years later (Rees *et al.* in press).

The movement of swans onto arable land, together with the increase in numbers wintering in Britain during the 1960s, 1970s and early 1980s, resulted in some conflict with farmers, particularly where the birds were feeding on winter cereals or Oil Seed Rape. WWT therefore co-ordinated a survey of changes in the distribution of all three swan species wintering in Britain and Ireland during the 1990-91 winter to assess the extent of the problem. Results showed that less than 15% of Whooper Swans and 3% of Mute Swans were on arable land during the winter, and that although 60% of Bewick's Swans were on arable crops these birds were congregated at a comparatively small number of sites (Rees *et al.* in press). Large flock sizes were associated with arable land for all three species, again indicating that whilst the presence of large flocks at certain sites may give the impression that swans feed mainly on farmland, the birds are actually more widely dispersed. Since the swans have clearly changed their feeding habits in the last three decades, however, the monitoring of feeding site selection should be continued in future years.

Inter-specific competition

One of the fundamental problems associated with managing a reserve is that conditions for one species may be attractive to others, leading to inter-specific competition for a limited food supply. The New Grounds, for instance, was originally established as a wildfowl refuge because of its importance to wintering White-fronted Geese *Anser albifrons*, but has since been used by increasing numbers of Bewick's Swans and European Wigeon *Anas penelope*. A study of the distribution of swans, geese and Wigeon at the New Grounds found that the Bewick's Swans tend not to use fields that have been heavily used by geese and/or Wigeon, probably because the presence of large numbers of geese and Wigeon resulted in a significant depletion in the biomass of vegetation (Rees 1990).

The fact that numbers of Bewick's and Whooper Swans increased at the same time at the Ouse Washes and at Martin Mere (**Figures 3** and **5**) suggests that the presence of the Whooper Swans was not deterring the smaller Bewick's Swans from using these sites. Whooper Swans monopolise the supplies of grain, and to a lesser extent the potatoes, provided on

WWT reserves, however (e.g. Black & Rees 1984), whilst the Bewick's Swans fly out to fields in the surrounding area to feed. The 1990-91 swan survey found no evidence to suggest that Bewick's Swans were avoiding fields used by Whooper Swans, with the number of single species and mixed species flocks simply reflecting the distribution of the two species within Britain and Ireland (Rees *et al.* in press). More detailed data concerning the distribution of the two species at Martin Mere have been collected to determine the extent to which Whoopers actively exclude Bewick's Swans from the reserve (**Figure 6**), and whether this affects the Bewick's Swan's feeding patterns and return rates in subsequent years. An earlier study of swans wintering at Caerlaverock found that Whooper Swans spent more time in feeding on grain than the other two species, and that the Bewick's and Mute Swans left the grain to start comfort activities whilst most of the Whooper Swans were still feeding (Black & Rees 1984). Moreover, the number of Bewick's Swans wintering at Caerlaverock has declined from 77 birds in the 1980-81 and 1981-82 winters to only small numbers recorded each winter during the 1990s.

Figure 6. Whooper Swan chasing a Bewick's Swan. Photograph by Philippa Scott.

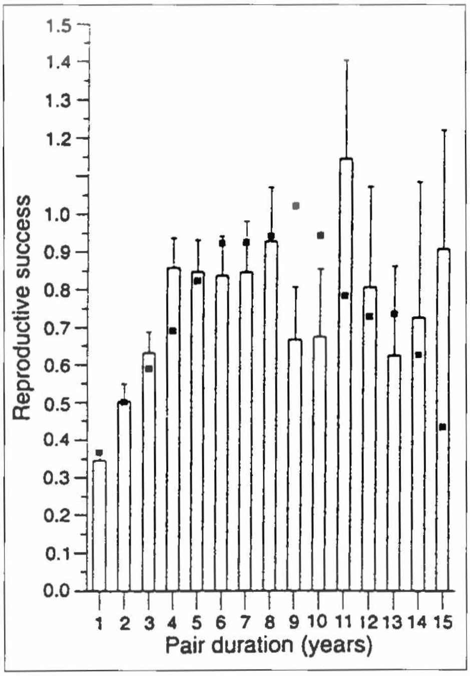
Biological principles addressed by the swan research programme

One of the main advantages of long-term single-species studies is that they can address a broad range of questions about the animals being monitored. The Bewick's Swan study therefore covers a variety of biological principles, although most effort so far has been directed towards social behaviour (including parental care and mate fidelity), migration and movements, feeding ecology and breeding biology. The Whooper Swan study is comparatively recent, commencing with the completion of swan-pipes or traps at Caerlaverock and Welney in 1980, and the resultant development of the Whooper Swan ringing programme. Recent analyses (e.g. Rees *et al.* 1996) found that, even after 14 years, the Whooper Swan databases do not yet hold the depth of information on longevity and individual lifetime reproductive success achieved by the Bewick's Swan study, since the swans have a very long life-span, and there is substantial annual variation in breeding success due to weather conditions. Whooper Swans are comparatively easy to study in the breeding range, since the Icelandic marshes are more accessible than the Russian tundra, and most of the Icelandic-breeding population winters in Britain and Ireland, making it possible to monitor the same individuals throughout their migratory range. Analyses of the Whooper Swan data to date therefore have concentrated on the birds' breeding biology (Rees *et al.* 1991; and especially Einarsson 1996), with the satellite-tracking of the swans' autumn and spring migration proving an exciting addition to the study (see below).

Life-history studies

When the Bewick's Swan study started little was known concerning the natural life-span of these birds, and thus the number of years of observations needed to determine their longevity and lifetime reproductive success. The maximum longevity recorded for wild swans wintering at WWT reserves is currently 26 years for Bewick's Swans and 14 years for Whooper Swans, although the lower Whooper Swan figure probably reflects the more recent development of the Whooper Swan study. Recoveries of Whooper Swans ringed in Iceland during the 1960s indicate that they also have a potentially long life-span, with some birds reaching at least 23 years of age (A. Petersen pers. comm.). With annual survival rates estimated at around 86-87% for Bewick's Swans (Evans 1979b; Scott 1988) and around 70-80% for Whooper Swans (Einarsson 1996), however, most swans do not reach "old age". Only 49 Bewick's Swans are known to have reached 20 years or older since the Slimbridge study started, of which 25 (51%) are female.

Figure 7. Association between pair duration and reproductive success in Bewick's Swans. Histograms and SE bars show mean reproductive success and black squares denote fitted values after controlling for year and age effects. From Rees, Lievesley, Pettifor & Perrins (1996).



Reproductive success in Bewick's Swans increases with pair bond duration (Scott 1988), even after controlling for age and year effects (Rees *et al.* 1996, **Figure 7**). Breeding success is also associated with male size and the dominance rank achieved by the pair in the winter flock (Scott 1988), presumably because size affects the male's fighting ability and thus his ability to secure the best breeding territory. A similar increase in reproductive success with pair duration occurs in Whooper Swans (Einarsson 1996; Rees *et al.* 1996), and long-term monogamy appeared to be more advantageous in some years than in others for both species. There is not yet any evidence from the Bewick's Swan study to suggest that breeding success declines in older birds (i.e. aged 20+); one of the oldest females, (named "Prongy") brought a cygnet to Slimbridge in her 26th year (**Figure 8**). Despite the advantages of mate fidelity, some 5.2% of Whooper Swan pairbonds end in divorce, although to date only one case has been documented for Bewick's Swans (Rees *et al.* 1996). Long-term pair bonds are thought to be especially important to Bewick's Swans, since the long-distance migration and shortness of the arctic summer means that they have little or no time for courtship and pair formation before the start of the breeding season. Most courtship activity appears to occur in the non-breeding flocks in the breeding range.

Social behaviour

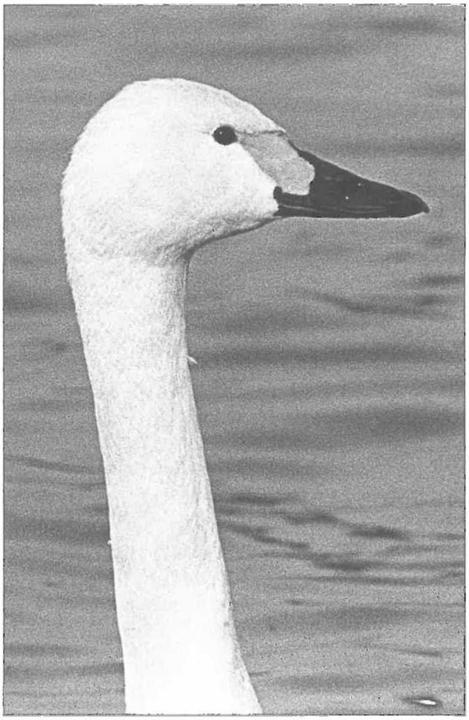
Much of the work on social behaviour of swans was based on observations of Bewick's Swans wintering at the Welney Wildfowl Refuge on the Ouse Washes, Norfolk (Scott 1978; 1980a;b;c). Swans are generally gregarious in winter, but may use simple threats or more ritualised displays (involving repeated vocalisations, head-pumping and wing-flapping) to establish the dominance of individuals, pairs or family units within the flock. Results showed that both members of a pair benefit from remaining together during the winter months, in terms of enhanced dominance rank in the flock and in time spent feeding in one anothers' presence, although females may benefit more than males (Scott 1980a).

Cygnets remain with their parents throughout the first winter, with family members departing together for the breeding grounds in spring (Scott 1980b). Although it seems likely that the nesting pairs become territorial in the summer months, and drive away any yearlings that try to remain with them, the young may again associate with their parents upon returning to the wintering range for up to their seventh winter.

Success in aggressive encounters is associated with the size of the social group, with families dominating pairs, which in turn tend to dominate single individuals. Parental care in the first winter proved important in protecting offspring from feeding competition from other individuals in the flock (Scott 1980b), which may also improve their chances of survival, particularly since the cygnets have not reached full adult size (Evans & Kear 1978) so would otherwise be low in the social hierarchy. Moreover, the young of dominant families were more successful in aggressive encounters than those from subordinate families when separated from their parents, in both their first and second winters, suggesting that cygnets acquire the dominance rank of their parents (Scott 1980b). Protecting the young involves measurable costs to the parents, however, particularly the male. Paired males with offspring spend more time being vigilant and in aggressive encounters than those without young, and are in poorer condition at the end of the winter, whereas the mates and offspring of dominant males spend more time feeding and developing fat deposits prior to the spring migration (Bowler 1994; 1996).

The pre-flight "head-bobbing" movements, performed by the northern swans prior to take-off, were examined to determine the function of the display (Black 1988). In addition to ensuring that members of pairs and family units leave together, the pre-flight signals attracted the attention of other swans in the flock, thus maintaining flock cohesion. They also reflected prior knowledge of the food available at the end of the flight, with swans spending less time performing pre-flight signals when flying to the grain feeds than when they flew to forage on grass (Black 1988).

Figure 8. "Prongy" - one of the oldest Bewick's Swans, who reached 26 years of age. Photograph by Philippa Scott.

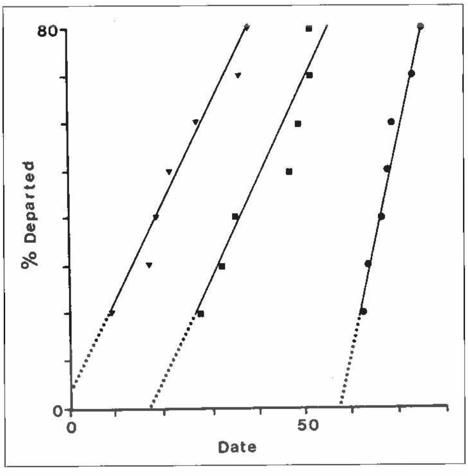


Monitoring migration

Although aspects of the Bewick's Swan's life cycle could be monitored without relying on artificial markings (individuals were identified by bill pattern at Slimbridge), a regular ringing programme was introduced in 1967 to enable information to be gathered from birds on migration and at alternative wintering sites (Evans 1982; Rees 1987). The ringing programme was extended to other areas, to include Whooper Swans by the building of swan-pipes at Welney (in 1980), Caerlaverock (1980) and Martin Mere (1990), and by catching swans at their breeding grounds in Iceland (from 1988) and Russia (from 1991) (Rees & Bacon in press). A preliminary analysis of the resightings of Bewick's Swans confirmed that cygnets continue associating with their parents during the early stages of spring migration, and that swans which had wintered at Slimbridge tended to use sites in western Germany as staging areas in the spring, at least until 1983 (Evans 1982). A more recent comparison of the migratory routes used by Bewick's Swans marked in different parts of the UK indicated that birds from Martin Mere and Caerlaverock have more northerly migratory routes than those from Slimbridge and Welney. Moreover, swans from Welney were only occasionally seen at sites further west (Rees & Bacon in press). Resightings of Whooper Swans in Ireland have shown that these birds are remarkably mobile, frequently moving between Britain and Ireland, as well as using several sites within Ireland, in a single season (McElwaine *et al.* 1995). Nevertheless Bewick's and Whooper Swans both show a high level of winter site fidelity, which should be borne in mind in efforts to conserve the species (Black & Rees 1984; Rees 1987). A conflict of allegiance may arise for newly formed pairs on their autumn migration, since pair formation usually occurs in the summer, and the new mate will usually have formed an attachment to a different wintering site. A study of swans resighted upon re-pairing indicated that males predominated in determining the wintering site for the new pair (Rees 1987), although the age and previous experience of the mate may also have an effect. Evidence from pre-flight behaviour suggests that there is a shift in responsibility within the pair-bond as the winter progresses and that, as in other species of waterfowl, the females determine movements to the nest site.

One of the more experimental (albeit retrospective) studies to emerge from the Bewick's Swan research programme was an assessment of how day length affects the timing of migration. Floodlights were installed along one side of the Rushy Pen at Slimbridge before the birds started using the pen, and were retained since the artificial illumination did not seem initially to affect the swans' behaviour. Changes in the floodlighting regimes had a significant effect on the timing of the Bewick's Swans' departure in spring, with birds leaving earlier in years when they were floodlit until 22:00 h than when they were illuminated until 20:00 h, and these birds in turn left before those receiving a natural photoperiod (Rees 1982; **Figure 9**). As a result of this study, the floodlights now fade at 18:30-18:45 h, and the Bewick's Swans at Slimbridge leave at around the same time as those in other parts of the UK. Although day length determines the broad migratory season, final departure is influenced by weather conditions (particularly wind direction, Evans 1979c; Rees 1982) once the birds have received sufficient photostimulation. Moreover, although photoperiod clearly had a major effect, the swans did not all leave on the same day; further investigations showed that individual birds were consistent in the timing of their arrival and departure every winter, indicative of individual response thresholds to the day length stimulus (Rees 1989).

Figure 9. Percentage of the Bewick's Swan flock wintering at Slimbridge that had departed on spring migration under three different light regimes. Dates are the number of days after January 1st. Light regimes: triangles - illumination until 22:00 h; squares - illumination until 20:00 h; dots - natural daylength. From Rees (1982).



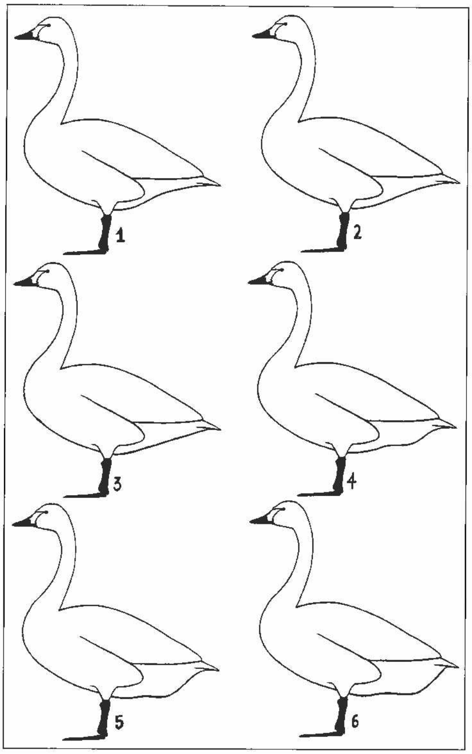
The use of satellite transmitters to track Whooper Swans migrating between the UK and Iceland in recent years, carried out in collaboration with Professor Colin Pennycuick of the University of Bristol, has provided new insight into the altitudes and speeds of migration and the amount of fat needed to complete the flight. A report by an airline pilot of swans (thought to be Whoopers) flying at 8,200 m off the Outer Hebrides in 1967, heading towards Northern Ireland (Stewart 1978), was surprising for birds with such a high body weight to wing area ratio. The satellite tracking of two female Whooper Swans flying from Iceland to Caerlaverock in autumn, and of two male birds from Caerlaverock to Iceland in spring, found that the birds may gain height to clear mountains, but during the sea crossing they flew at low altitudes and landed on the water in adverse weather or poor visibility (Pennycuick *et al.* 1996). Moreover, although the two females flew straight from Iceland to Scotland, taking 11 h 20 min and 13 h 45 min respectively, the two males were both diverted from their original track by gale force winds, and one was at sea for four days (Pennycuick *et al.* 1996). The study is continuing, however, and may yet find that Whooper Swans migrate at high altitudes under certain conditions.

Feeding ecology

The feeding ecology of the migratory swans has been studied at WWT Centres on the Ouse Washes (Owen & Cadbury 1975; Scott 1980c), at Caerlaverock (Black & Rees 1984; Einarsson 1996) and at Slimbridge (Rees 1990; Bowler 1996), in an effort to understand the habitat requirements of the swans and to improve the carrying capacity of the reserves. At Slimbridge for example, Bewick's Swans occurred most frequently and in greatest numbers in fields with the highest biomass of green vegetation (Rees 1990). The percentage of protein in vegetation was a relevant secondary factor, and a preference for flooded pasture was also shown, although the absolute depth of flooding did not appear to influence site selection. More recently, Bowler (1996) demonstrated that swan distribution was determined primarily by the extent of flooding, with swan use increasing as the area of flood water increased. However, birds from two distinct roost groups at Slimbridge selected fields in different ways. Swans from one roost group selected flooded fields with a high level of protein in the sward, whilst those from the second group simply used fields close to the roost, low in both protein and biomass. These differences in feeding site selection also reflected differences in foraging behaviour. At the second roost site, birds were able to feed for longer periods and on larger amounts of provisioned grain (usually wheat) per swan, than those at the first roost site, and their selection of feeding sites during the day therefore was less critical (Bowler 1996). Similarly, Whooper Swans which remained on the refuge at Caerlaverock, and fed on barley distributed at the site, spent considerably less time feeding than those at the neighbouring traditional grassland site of Islesteps (Black & Rees 1984).

Grain is provided at the swans' roost sites at all WWT Centres where migratory swans occur in large numbers. In most cases the grain probably forms a major part of the diet only during prolonged periods of freezing weather, especially at Welney and Martin Mere where the Bewick's Swans usually fly out at dawn to feed in the fields, but its presence does encourage birds to use the refuges and to return in subsequent years. At Slimbridge, adult Bewick's Swans spend only one third of their time on the fields actually feeding, with one third spent resting and one third in other activities (Bowler 1996). Birds feed more intensively at migratory sites in the spring; flock scans at Matsalu Bay in Estonia found that on average 59% of the birds were feeding and 24.5% were sleeping, reinforcing the view that the site is important to the birds for resting and replenishing their nutrient reserves during spring migration (Rees & Bowler 1991). Feeding activity at Slimbridge peaked in early February when food availability was low and climatic

Figure 10. Abdominal profile scores for Bewick's Swans, used for assessing body condition in the field: 1 - Very Concave; 2 - Concave; 3 - Straight; 4 - Convex; 5 -Very convex; 6 - Sagging. From Bowler (1994).



conditions at their worst. Increasing protein levels in the swards at the end of the winter also led to an increase in the number of swans seen feeding, perhaps because they were developing fat reserves to fuel their spring migration. An estuarine food source (an amphipod *Corophium* spp. and/or a polychaete worm *Nereis* spp.) was also used at this time (Bowler 1996).

Detailed feeding studies have highlighted different foraging strategies used by individual birds. Males spend less time being vigilant and feed more intensively when grazing on swards with a high protein content. They invest more effort in protecting their mates and/or offspring from intra-specific feeding competition when food quality (in terms of protein levels in the sward) is low (Bowler 1996). Female Bewick's Swans generally spend more time feeding than males, and have faster peck-rates and slower step-rates. Female abdominal profiles (indicative of body condition, Bowler 1994 and **Figure 10**) at the end of the winter is associated with the dominance rank of the pair, and also has a significant effect on subsequent breeding success as measured by the presence or absence of cygnets in the following winter (Bowler 1996).

International collaboration

Although WWT's swan research programmes have concentrated mainly upon observation of birds made at WWT Centres, international links have been a major part of the study, initially through sightings of ringed birds reported by ornithologists in other parts of Europe, then through co-ordinated international censuses, and more recently through collaborative studies of the swans' breeding biology. Expeditions to ring Whooper Swans on their breeding territories, and to monitor their breeding success, have taken place every year since 1988, with nest-checks being undertaken by Icelandic colleagues from 1990 onwards. Similarly, joint expeditions to study Bewick's Swans nesting on the Russki Zavorot peninsula in the Nenetski National District, Russia, have been undertaken since 1991, involving scientists from the All-Russian Research Institute for Nature Protection, the Komi Science Centre, the University of Groningen, the Danish Ministry of the Environment and WWT. Communication at an international level is of vital importance for the effective conservation of migratory waterbirds, including swans, since habitat loss in one area is likely to affect numbers and distribution elsewhere, particularly for the Bewick's Swan which is concentrated at comparatively few sites (Beekman *et al.* 1994). Bewick's and Whooper Swans have been protected from hunting for many years, but political changes within the former USSR make the situation more uncertain and the shooting of both species has recently been legalised in Yakutsk, under regional law. Also, although the effects of climate change associated with global warming are still being debated, there is a risk that changes in habitat and farming practice would increase the conflict with farmers and bring the birds closer to man-made hazards in a more closely managed environment. Swans, like other large birds, have a low reproductive rate, making them vulnerable to increases in mortality and decreases in breeding success. Bewick's Swans are also difficult to breed in captivity; the long days of the arctic summer may be needed to trigger the start of the breeding programme (Murton & Kear 1978). It is therefore important to continue monitoring changes in population levels and distribution so that further conservation measures may be introduced before it is too late for them to be effective.

Since the Bewick's Swan research programme commenced in 1964 the following people have been involved at Slimbridge in the individual recognition of swans by their bill patterns (in chronological order): Peter Scott, Philippa Scott, Dafila Scott, Pat Pollard, Maya Scull, Tom Pitcairn, Mary Evans, Eileen Rees, John Bowler and Sue Carman. Records of individual swans at Welney were maintained by Barbara Wager, Dafila Scott, Josh Scott, Don Revett, Jonathan Revett and Linda Butler. The Caerlaverock Whooper Swan data have been obtained by Colin Campbell, Rick Goater, Barry Sears, David Campbell, Jeff Black, Paul Shimmings, Richard and Carol Hesketh, and Olafur Einarsson. Sightings at Martin Mere were collated by Chris Tomlinson, Charlie Liggett and Eileen Rees, with major contributions by Wayne Shields and Ron Barker. Most of the fieldwork in Iceland has been undertaken by Olafur Einarsson, in collaboration with Sverrir Thorstensen, Skarphedinn Thorisson and Johann Oli Hilmarsson, with support from the Icelandic Museum of Natural History (especially Aevar Petersen), the University of Iceland (especially Arnthor Gardarsson) and the Icelandic Research Council. Fieldwork in Russia would not have been possible without the efforts of Yuri Shchadilov of the All-Russia Research Institute for Nature Protection, the valuable assistance of Anna Belusova, Yuri Morozov, Sergei Petrusenko and Mr Kotkin, and the co-operation of Jan Beekman, Yuri Mineyev and Pelle Andersen-Harild. We are extremely grateful to the very many people who report their sightings of ringed birds upon which the study depends, and particularly for the efforts over many years of Carl Mitchell, Chris Spray, Andrew Bramhall, Jim Wells, Graham McElwaine, Kendrew Colhoun, Oscar Merne, Trinus Haitjema, Wim Tijsen, Jan Beekman, Gert Dahms, Helmut Eggers, Leho Luigujoe, Pelle Andersen-Harild and Bjarke Laubek.

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