Structure and dynamics of a Mute Swan population

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This paper gives data on numbers and breeding of Mute Swans Cygnus olor in the Uists and Benbecula (Outer Hebrides islands, Scotland) for 1971-1974. These data are of interest when compared with studies of Mute Swans elsewhere (Perrins & Reynolds 1967; Minton 1968, 1971; Scott and the Wildfowl Trust 1972), but, unlike those, Swans in the Uists are wild birds, living naturally with minimal assistance or interference from man. These data may also help to provide a base line from which to judge the effects of development in these islands, where conservation interests may be at risk, but where there is little other quantitative information on wildlife.

Counts were done within a 2-day period in the first week of each month. In the course of previous research, all lochs on the three islands were visited, and since Mute Swans were not seen on the numerous, biologically poor, oligotrophic lochs, only the eutrophic, mesotrophic and saline lochs were checked in this study. This was an easy task as most of these could be reached by car. Nearly all counts were done by C.B., with only occasional checks by the other authors. It was important to get round all the lochs in a short time and a very few lochs only accessible by foot which sometimes held a swan or two were not visited. Discounting any swans that may have been missed is unlikely to have led to important errors of interpretation. Care was taken to distinguish Mutes from Whooper Swans Cygnus cygnus which visited the islands in winter. We have no measure of the accuracy of counts, but adult swans are obvious birds and most counts are probably accurate within about 5%. However, a few apparently low counts (* in Table 1) suggest that some swans may have been missed on rare occasions.

The lochs varied greatly in size but this paper is not concerned with the population density of swans. The aim was to cover the same lochs every month and thus obtain comparative information on swan numbers and productivity. 'Full-grown' (i.e. white) and young (i.e. brown) swans were distinguished from May-June to December, but since some first-year Mute Swans became white from about December onwards, the two groups were not separated from January.

Lochs were classed as saline if they were

sea-lochs or under tidal influence. This last category included several lochs which were almost entirely enclosed but which at high tide had a narrow connection with the sea. In such lochs, salinity decreased with distance from this exit. Eutrophic lochs were on the calcareous shell-sand machair, mostly on the west and north sides of the islands. Mesotrophic lochs were on low ground between the machair and peaty hills. They were considerably less acid, and supported more vegetation, than the oligotrophic lochs of the peatland.

Results

1. Full-grown birds

Most swans were seen on N. Uist and S. Uist, with usually only about 20-30 birds on Benbecula and little variation there through the year. Each year in 1971–1974, the pattern of the counts was much the same (Figure 1, Table 1); lowest (380-460) in December, with a small increase in January-February (by 100-175 immigrant birds). It was then fairly stable at 470-560 till April or May, when there was a second big increase of up to 200 more immigrants. Numbers reached a peak for about two months around July-September (640-750), and then a twostage decrease occurred to October (510-580) and December. Counts were very similar at certain periods each year. In 1971, 1973 and 1974, the December totals were between 371-398; in 1972-1974, adults in June totalled 572-574, and were not much different in 1971; and the October figures were also similar each year.

Details of the monthly counts of full-grown Mute Swans on the two main islands summarized in relation to loch type are deposited at the Nature Conservancy Council, Inverness. There were variations both between and within years particularly on the big saline lochs in S. Uist. Most swans occurred in flocks on these saline lochs. These variations in the numbers of swans on the saline lochs accounted for most of the pattern shown Table 1, for they were mostly due to changes in swan numbers on L. Bee in S. Uist and on a few sea lochs in N. Uist, particularly L. an Duin and the nearby complex of partly enclosed sea lochs near Lochmaddy. Counts

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Table 1. Numbers of Mute Swans counted on the Uists and Benbecula in 1971-1974.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1971	447	563	488	no d	ata	633	625	734	693	548	431	335
1972	556	510	514	548	521	572	582	683	668	565	466	424
1973	554	535	521	477	597	574	709	756	608	511	330	329
1974	385	496	470	523	455*	574	641	566	540	576	385	356
Average over												
4 years	485	526	498	516	524	588	639	685	627	550	403	381

B. Young counted in June-December

1971	123	145	138	128	143	100	36
1972	90	161	63*	91	94	62	35
1973	185	179	157	136	127	97	69
1974	153	158	106	96	90	46	- 30
Average over							
4 years	115	161	116	113	113	76	43

C. Totals, averages (A+B) over 4 years

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485	526	498	516	524	703	800	801	740	663	499	424

[†] by our definition young swans became full-grown on 1st January of their first year, see text. ^{*} these figures are apparently low, suggesting that unusually many birds may have been missed.

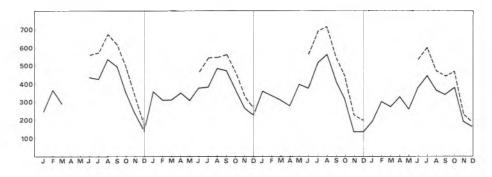


Figure 1. Numbers of Mute Swans in the Uists and Benbecula, Outer Hebrides, from monthly counts in 1971–1974. Continuous line—full-grown (white) birds; broken line—total birds, including young (brown) birds. From January each year all birds were classed as full-grown (see text).

for L. an Duin and L. Bee are given in Table 2. These data for L. Bee show a similar pattern each year, with an increase of about 200 after March and a peak around June-August, and with numbers much the same each month in most years. An exception was found in November-January 1973-1974, when low numbers were associated with severe gales. There was no such consistency at L. an Duin, where variations appeared to be unpredictable.

Altogether 86 lochs were used by paired

birds in spring and other lochs by nonbreeders in flocks. Details are deposited. Some lochs held more than one pair, giving a maximum of 110 potential breeding places in these years, but most lochs (53 altogether) supported only one breeding pair. In different years, up to 14 lochs sometimes had two pairs, seven lochs sometimes had three pairs, and L. Kildonan in 1972 and L. an Duin in 1973 had four pairs. The number of pairs depended on the size of the loch, but promontories and islands offering safety from distur-

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
L. Bee												
1971	199	258	194	no c	counts	432	424	393	299	198	no count	145
1972	176	203	244	260	260	339	263	415	383	264	213	179
1973	191	197	191	269	284	325	403	425	340	247	74	38
1974	69	181	181	238	240	331	419	413	350	293	120	105
L. an Duin												
1971	no count	23	57	95	71	87	67	112	43	31	9	28
1972	49	67	99	14	63	85	70	111	61	71	63	86
1973	67	18	18	29	76	52	83	62	73	23	31	63
1974	33	84	84	83	39	36	11	9	32	43	43	61

Table 2. Numbers of full-grown Mute Swans counted on L. Bee, S. Uist and on L. an Duin, N. Uist in 1971–1974.

Table 3. Data on breeding production of swans in the Uists and Benbecula in 1971-1974

	1971	1972	1973	1974	Mean
Nos. of lochs with one or more pairs in March	65	64	67	68	66
Total swans in March	488	514	521	470	498
Nos, of flocked birds in March	320	338	353	300	328
Nos. of pairs in March	86	89	84	84	86
Nos. of pairs with young in Sept/Oct	38	47	39	32	39
Max. nos. of young in June/July	145	161	185	158	162
Max. nos. of young in Sept/Oct	143	94	136	96	117
Nos. of young in Dec	36	35	69	30	42
Nos. of young/productive adult in Sept/Oct	1.68	1.02	1.74	1.50	1.48
% loss June/July to Sept/Oct	1.4	41.6	26.5	39.2	27.8
% loss June/July to Dec	68.9	78.3	62.7	81.0	74-1

bance by people and the possibility of isolation from other swans were probably also important.

There were 84–89 pairs in each of the four springs (Table 3). Of these, 39 pairs (45%) on average produced young on 37 lochs. The number of productive pairs varied from 32 in 1974 to 47 in 1972. Saline, mesotrophic and eutrophic lochs were used by breeding swans, apparently in proportion to their availability on the different islands.

2. Breeding and numbers of young

The maximum numbers of young counted in September–October are taken to be the numbers reared. There were no obvious differences between the productivity of the different types of lochs in terms of young produced per pair in spring, nor between the numbers of young produced per pair on each island. The most productive lochs on the islands in terms of the numbers of young reared over the four years are listed in Table 4. These include examples of all three habitat types, and are mostly large lochs (with relatively high productivity partly associated with more pairs breeding). But some large lochs (e.g. Fada, Benbecula; Grogarry and Hallan, S. Uist) failed to produce many young swans and more work is needed to understand why.

On average 46 paired birds produced no young, but some of these may have nested and failed. The total number of unpaired nonbreeders was remarkably constant, varying between only 374 and 415 over the four years, and averaging 387. Most of these birds were in flocks, and a list of the principal lochs carrying non-breeding Mute Swans is

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 Table 4. Lochs on which 10 or more young were reared during the period 1971–1974

Loch	Grid ref.	Type of loch	No. reared
N. Uist			
Oban na Curra	830635	Saline	10
Alioter	887723		10
An Strumore	897697		16
Lochmaddy	907680	17	12
An Duin	890740		14
Dlavat	755755		15
Nam Feithean	712705	Eutrophic	12
Scarie	718706		14
Sandary	735685	**	17
Benbecula			
Dun Mhurchaidh	795545	Mesotrophic	11
Dlavat	810555	mesonopine	14
Na Liana Moire	762533	Eutrophic	16
Dban Liniclett	785500	2011 0 p	10
S. Uist			
Ceann a' Bhaigh	760305	Saline	13
See	790425		22
	770440		22
Druidibeg	790375	Mesotrophic	16
Ollay (mid and east)	755315		29
	768315	**	27
tilligarry	760390	Eutrophic	14
orornish	735305		18
Eilean an Stadir	733260		10
Ollay (west)	740330		11

Note. Other lochs which had 15 or more cygnets on them in July, from which birds may have moved by September-October, include:

N. Uist: Oban nam Fiadh, saline (19); Fhaing, saline (17).

S. Uist: Grogarry, eutrophic (15); Ardvule, eutrophic (19); Hallan, eutrophic (16).

deposited. Only L. an Duin and L. Bee regularly had flocks or more than 50 swans, but another three (Strumore, Nam Fiadh, and Ollay (mid)) regularly supported 10–50 birds. Altogether 26 lochs sometimes had flocks of more than ten birds in the three years 1972–1974 for which the data are complete.

Discussion

1. Numbers of adults

In round figures, the three islands held about 500–550 full-grown swans in spring (February–April) and in autumn (October), compared with a maximum of about 750 in July. The number of paired birds in spring was remarkably constant (Table 3) as well as the spring and autumn totals. The productive pairs made up about 15% of the totals in spring and autumn and 10% in July. These proportions are considerably less than the national average of about 40%, based on a national census done in 1955 and 1956. (The

'breeding population' was estimated at 3,500-4,000 pairs, with another 11,000 or more non-breeding birds (Scott et al. 1972).) This difference is associated with the large numbers of non-breeders on the Uists, which in turn depends on the abundance of habitat suitable for flocks. Another important characteristic of the Uists is the big annual increase in the numbers of full-grown swans on L. Bee in June-September. These birds moulted there. Fluctuations in numbers elsewhere in the Uists do not account for this big increase. The origin of these immigrant birds is unknown, but L. Bee may be important for the conservation of mute swans over a wider area than the Uists and Benbecula. Breeding Mute Swans occur only in the Uists and Benbecula in the Outer Hebrides, and on very few of the Inner Hebrides. They are also rare in the west of Scotland except for the Clyde area (Atkinson-Willes 1963). It seems likely therefore that the Mute Swans moulting on L. Bee come a considerable distance

across the sea, perhaps from south-west Scotland or northern Ireland.

The general stability in the numbers of dispersed pairs in different years can presumably be explained by territorial behaviour, with young of the year gradually dispersing during the winter. But territorial behaviour cannot account for consistency in numbers of flocked (non-breeding) birds, mainly on saline lochs. Possibly the numbers of these birds were adjusted to their food supply which may not have changed much from year to year, except for an annual increase in July-September, and perhaps an annual decrease in November-December. Many Whooper Swans were also present in autumn and early winter, and fewer in late winter, partly in the same places as Mutes. The variability in numbers of Mute Swans around mid-winter may have been due to food shortage, competition with Whoopers, or to periodic bad weather causing movement. The variable numbers on saline lochs in the sheltered north-east of N. Uist were linked with periodic gales which had most effect on more exposed lochs (ice was not recorded). Large numbers of birds were sometimes seen around Lochmaddy following gales from the west, with subsequent decreases when the gales subsided. Occasional decreases in the totals may also have resulted from some swans temporarily leaving the islands altogether. On most freshwater lochs, numbers were relatively small and the movements of a few birds caused disproportionately large changes.

2. Production of cygnets

The numbers of young per parent varied in different years from $1 \cdot 0 - 1 \cdot 7$ and averaged $1 \cdot 48$ (Table 3). This average ratio of about $1 \cdot 5$ young birds to 1 old bird up to October was higher than around Oxford where it was about 1:1 (Perrins & Reynolds 1967). The Oxford population was declining, whilst the Uists population was stable, but the decrease in the former was largely attributable to accidental deaths of adults (Scott *et al.* 1972).

Only 25 out of 59 lochs occupied by productive swans produced 10 or more young altogether over four years. Egg or cygnet mortality was presumably high. With an average clutch of six eggs (Scott *et al.* 1972), the mean breeding population of 55 pairs would be expected to lay on average about 330 eggs. The highest number of cygnets seen was 185 (though the real totals would have been greater than the numbers seen on any one occasion). Thus the mortality between egg-laying and the time when cygnets were first seen (i.e. about one month old) was probably about 40%. This compares with an average 28% loss between July and September-October, but this varied from practically none in 1971 to 42% in 1972.

The original counts (Figure 1) show a much bigger monthly loss after September than before, but this was probably due chiefly to emigration. The December totals were very similar in 1971, 1973 and 1974, and in 1972 and 1974 the numbers including young were almost exactly the same as the November totals without them. This suggests that the total number may have been regulated in December, partly by the exclusion of young.

3. Further work

Although the accuracy of the counts is not known, we think that these conclusions about the year to year stability of swan numbers in the Uists in 1971-1974 are valid. More frequent checks on the counts would nonetheless be worthwhile. It would also be valuable to have information on mortality in adults. One would expect this to be low in an undisturbed area with few overhead wires, an important cause of mortality in south England, and would enable more detailed comparisons to be made with studies at Oxford and elsewhere (Perrins & Reynolds 1967; Minton 1971). Large scale ringing would be needed. This is practicable on L. Bee and it might also show the origin of the immigrant moulters. Other studies might be done on the inter-relations between the swans and their food, to try to explain the remarkable seasonal and annual constancy of swan numbers. Knowledge of the productivity and food potential of their food plants might be valuable in conservation work elsewhere. Finally, the swans presumably interact together in bringing about the apparent regulation of numbers in the non-breeding flocks, and the behavioural mechanism achieving this regulation should repay study, as should their relationships with wintering Whoopers.

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Summary

1. In 1971–1974, the Uists and Benbecula contained up to about 750 full-grown Mute Swans *Cygnus olor* in August, about 500–550 in spring and autumn, and about 400 in December. These figures were remarkably similar each year.

2. On average, about 20-22% of the spring stock produced young. Non-breeders were numerous, and were found mainly in flocks on saline lochs.

3. The numbers of non-breeders were augmented each July–September by about 200 birds which came to the islands to moult, mostly on Loch Bee.

4. Breeding and non-breeding swans occurred on three main types of loch, eutrophic (machair), mesotrophic (other farm land) and saline (connected with the sea). They were absent from the numerous oligotrophic lochs. Loch Bee in S. Uist and the Loch an Duin complex in N. Uist were especially important saline areas for flocked swans.

5. Constancy in the numbers of dispersed pairs was attributable to territorial behaviour, but constant numbers of flocked birds in given months in different years must be due to other behaviour, possibly involving some other adjustment to food.

6. Among pairs that produced young, the ratio of young to old was similar on all three types of loch.

7. Overall, the ratio of young produced per successful breeding pair varied in different years between 1.02-1.74 per breeding adult.

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