A study of the Abbotsbury Mute Swans

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Introduction

The Mute Swans *Cygnus olor* which form the basis of this study live on a tidal lagoon known as the Fleet, in Dorset, southern England. The Fleet is about 14 km long, varies in width between 100 and 1,000 m, and covers about 480 ha. It is connected to the sea at its eastern end, in Portland Harbour, but separated from it for the rest of its length by a high pebble beach, the Chesil Bank. The water is mostly very shallow, (<2 m depth), but rather little mud is ever exposed, particularly in the western half, as the outlet to the sea is too narrow to allow the Fleet to empty completely at low tide. Because of this, and the inflow of a number of small streams, the Fleet has a lower salinity than the sea, varying from almost completely sea water at its mouth (33·8‰ salinity) to only brackish (19·5‰) at its western end, Abbotsbury, where the swans nest.

There is extensive growth of aquatic vegetation in the Fleet, especially eel-grass *Zostera* (three species) and wigeon-grass *Ruppia spiralis*. Although these die down during the winter, there seems to be sufficient for the swans to maintain themselves; they are rarely seen out of the water grazing on adjacent fields as is the case with swans on many inland rivers. The food supply may be damaged or reduced by high winds or ice: at such times feeding may be more difficult. Also utilizing these food resources in winter are about 5,000 Wigeon *Anas penelope* and 3,000 Coot *Fulica atra*.

There have been breeding swans on the Fleet for a very long time. Historically swans are valued highly as food and, at one time, all Mute Swans in Britain were the property of the Crown. Over the centuries, gifts of 'Swan Royalty' to various families of importance led to an elaborate and complex ownership system, each owner giving his swans distinctive bill-marks in order to identify them (Ticehurst 1957). The Abbotsbury swans are the most famous locally-owned population. In 1023 King Canute gave an area around Portesham (3 km N.E. of Abbotsbury) to a follower called Orc. This gift presumably included Abbotsbury since at a later (but unspecified) date Orc founded the monastery at Abbotsbury. Whether or not this ownership conferred rights to the swans is not known, but the Abbot laid claim to many wild animals on the property and also rights on the Fleet and the foreshore. The water is now owned by the Ilchester family who were given it in about 1526. The earliest record of the swannery (that we know of) is in 1393 when the court rolls of the Manor of Abbotsbury record that a 'William Squilor, *keeper of the swans*' (our italics) 'stirred up the water under the bridge "de la Flete" with "les hacches" so that the water overflowed "le Flete" and is so high that it washed against the nests of the swans of the Lord and moved and destroyed the eggs of the Swans'. This suggests that not only was there a swan-keeper at this time, but that already a fairly complex system of water control had been evolved in order to protect the nesting swans. When this custom was first started does not seem to be recorded.

Accurate censuses of the swans were not kept. However, in 1591, when there was a dispute between Queen Elizabeth I and the then owner of the Fleet, it was stated that there were 'Five Hundred Swans of which Four hundred and ten are white and Ninety the residue etc. are Cygnets'. (Incidentally, 'every pair of the Swans and Cygnets aforesaid one with another are worth Two shillings and sixpence"—Muniments of Ilchester.) This number is not so very different from that observed in some recent years (see below).

In the past, the population was managed to provide food for the estate and certain management techniques, which date back to those times are still in use, and need to be borne in mind when reading this paper. The swans nest in a single colony in an area of about 1 ha with only a very few isolated nests (most of these are in the same bay as the colony at the Abbotsbury end of the Fleet; none have nested successfully further east during the 12 years of our study). The birds nest on piles of cut reeds *Phragmites* which are put out for them (they will sometimes move the reeds a short distance); they nest as close as 2–3 metres and are notably unaggressive towards their neighbours. The colony size varies markedly for reasons which we do not fully

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understand. The maximum recorded number of nests is 130 in 1885, but in recent years the number of nests has been as low as 19 (1969) and as high as 100 (1980); 92 in the colony and 8 outside it.

The management procedure is as follows: the first young to hatch are put, together with their parents, into small pens (c. 5 m × 5 m). Cygnets of the further broods are added to these families until each pen contains between 15 and 20 cygnets plus one pair of adults. There were five such pens until 1976, when two more were added, so that 100–140 cygnets may be retained. The young birds are raised on chick-crumbs, eel-grass, grass-clippings, grain, etc, until mid-September when they are released (historically they would have been held and fattened for the table).

One of the curious features of the colony is the very low survival of cygnets raised outside the pens. The parent birds take these young down to the water and look after them in the normal way. However, the many non-breeders present harass them persistently, and most of the young are lost within one to two weeks. Even those pairs which nest away from the colony are rarely successful. In 1980, when 100 pairs started to nest, only 105 cygnets were raised, 89 in the pens and 16 on the Fleet. Since there is an upper limit to the number that can be raised in the pens (104 has been the largest number during this study), the breeding output of the colony can be said to vary in a density-dependent manner; except with very low breeding numbers, the larger the number of eggs laid, the lower the percentage which survive.

The total number of swans on the Fleet is at its lowest at the start of the breeding season (around 500, Table 1), but increases during the summer as birds arrive for their annual moult in July and August. While some of these then depart, they are outnumbered by further arrivals, mainly non-breeders, but including some family parties, which bring about a December peak of 800–900 (though over 1,200 in December 1980). The origin of these immigrant birds is still not clear (see below).

We have also included in this study the swans that are found on Radipole Lake, Weymouth, about 3 km away, since they intermix freely and can, to some extent, be considered as a single population. Radipole Lake is about 100 hectares in extent. The southern end is almost devoid of plant-life and much used for recreation but the northern area is more natural and is surrounded by extensive *Phragmites* reed-beds. This end of the lake also holds a number of other waterfowl in winter.

Table 1. Spring low numbers and winter peaks of swans (the Fleet and Radipole Lake combined) with totals of immigrant cygnets and adults.

Year	Spring Minimum a	Winter Maximum b	Winter max. of cygnets c	Total of local cygnets d	Immigrants Cygnets c–d	Immigrants Adults b–(c–a)
1969	480	783	129	102	27	175
1970	419	835	151	88	63*	265
1971	496	855	93	64	29	266
1972	533	813	118	48+	70	162
1973	508	733	71	78	−7	154
1974	498	821	113	85	28	210
1975	495	898	142	100+	42*	261
1976	488	832	99	114	−15*	245
1977	330	794	108	99	9	356
1978	509	832	138	113	25*	185
1979	572	949	146	114	32	231
1980	545	1,238	192	118	74	501

Notes.
1) Spring minima usually occur in May, winter maxima in November or December.
2) In the years marked with an asterisk, the survival of the cygnets on the Fleet is known to have been particularly poor.
3) The 1972 and 1975 totals of Abbotsbury and Radipole cygnets are minima as 24 and 29 cygnets respectively were present on the Fleet at the colony in June of each year and some of these may have survived to the autumn.

About 20 pairs of Mute Swans attempt to breed at Radipole in most years. The nests are often quite close together though, in contrast to those at Abbotsbury, they are not usually in sight of one another since they are built in the reed-beds. There is normally some territorial behaviour by the males, but territories are tiny in comparison with most Mute Swans breeding elsewhere in Britain. Breeding success is usually very low.

There is a marked seasonal pattern in the number of swans at Radipole. The numbers build up steadily after the New Year, but in early spring there are not very many birds apart from the breeding pairs. During the summer, numbers continue to increase until at the time of the moult (July–August) there have been as many as 180 birds; in recent years numbers have been rather lower (Table 1). After the moult, the numbers steadily decline and, once the young can fly, numbers drop rapidly until, by December, most or all of the birds have left. The large majority of these birds winter on the Fleet.

Within the close vicinity there are few other suitable nesting sites. However, the River Frome which runs across Dorset to Poole carries a small number of pairs (up to six within 25 km of the Fleet). To the west, there are few swans until the Exe estuary, some 56 km away, where small numbers of ringed swans from Abbotsbury have been recorded. To the east there are large concentrations of Swans at Poole and Chichester (some 40 and 60 km distant), which have been extensively ringed by other workers. There is some interchange between these flocks and those ringed in this study, but it seems to be less than 5%. We are thus dealing with a fairly closed population. Nevertheless there are immigrants into the population on a quite considerable scale (see below).

We have further evidence, from the results of a genetic study, that the population may be isolated. Analysis of blood proteins of the birds at Radipole and Abbotsbury has revealed the presence, in about 25% of the population, of a genetically determined isozyme of lactate dehydrogenase that is normally present in only about 1% of Mute Swans in Britain. Further details of this situation will be described elsewhere.

Our study commenced in October 1968. Visits have been made at roughly monthly intervals, being slightly less frequent in the winter, more regular in the summer. On each of the visits we have counted the birds on Radipole and the Fleet, separating the birds into 'white birds' (not born in the previous breeding season) and cygnets (by mid-December a few cygnets are so white that they are difficult to recognize at a distance). From the beginning, we have been able to ring freely at Radipole. In addition, starting in 1970, we have ringed some of the cygnets reared at Abbotsbury (except those taken out on to the Fleet by their parents) and since 1976 all of them. Since 1977 we have ringed many or most of the breeding birds there as well. We have used standard metal rings supplied by the British Trust for Ornithology and large-numbered plastic (Darvic) rings which could be read at a considerable distance (Ogilvie 1972).

In general we do not know the origin of birds which were alive and full-grown when ringed. However, there is one important exception to this. On the release of the cygnets at Abbotsbury (or on hatching for most of those not put in the pens) it has been traditional for the swan-herd to make a small nick in the front edge of the foot web to signify ownership. This mark normally remains visible throughout the life of the bird. Hence it has always been possible for us, on catching an unringed but web-nicked bird, to know that it had been raised at Abbotsbury. It is possible that sometimes birds escaped being marked, especially those that were brought up by their parents on the Fleet. However, we believe that such instances have been infrequent and in this paper we accept that a bird with un-nicked webs was raised somewhere other than Abbotsbury.

Swans living in this area do not face many of the hazards encountered by other swans in Britain. Two of the major causes of mortality elsewhere are from lead poisoning (caused by swallowing lead angling weights) and by collision with man-made objects especially overhead cables (Birkhead 1981; Ogilvie 1967). There is a certain amount of fishing on Radipole Lake and birds flying in and out of this water can, and sometimes do, collide with objects, especially bridges. On the Fleet, there is no coarse fishing and no overhead obstructions whatsoever. Hence the causes of mortality are strikingly different from those elsewhere in Britain. Foxes *Vulpes vulpes* take a number of eggs at Radipole and some occasionally at Abbotsbury. They also eat some swans on the Fleet. However, it seems probable that such birds were already sick or dead onshore. It is

difficult to believe that a fox could take a healthy swan on the water. Other predators are probably unimportant though a small predator, possibly a mink, *Mustela vison*, took 14 cygnets from the pens in 1980. Although as recently as 1272 the Abbot of Abbotsbury claimed to have 'free chace for wolves throughout all his land', none have occurred during this study.

Population size

In this section we discuss fluctuations within years, between years, and in breeding numbers, in that order.

We have already mentioned that there is considerable movement of birds between the Fleet and Radipole Lake. On the Fleet numbers are lowest about May, increase during late summer as birds come in for the moult, and the increase still further during winter reaching a level well in excess of the total found in early summer on the two waters (Table 1). Clearly there is immigration from other areas, the 'extra' birds (columns 6 and 7) may exceed 300, exceptionally 500. We do not know from where these birds come. A few come from nearby rivers and lakes, but the Dorset population as a whole is not sufficient to account for all the immigrants (Ogilvie 1981). They must therefore be coming from a still wider area. Since we cannot catch the birds in winter and we have only recently succeeded in ringing the immigrant birds during the moult, we do not yet have enough recoveries to indicate the extent of the area from which they are drawn. As already mentioned, the well-ringed population to the east, centred on Poole and Christchurch harbours, and the rivers in their hinterland, shows little interchange with the Fleet birds. The numbers of the estimated 'excess' are minimal since they are calculated on the basis that there is no mortality in the Radipole/Fleet population between September and mid-winter. This is obviously not true and in the case of the cygnets, many of which may die in their first few weeks after release on to the Fleet (Table 7), may be seriously at fault; at least in some years the numbers of immigrant cygnets are likely to be much higher than shown. Using data from other studies (e.g. Perrins & Reynolds 1967, Bacon 1980, Coleman & Minton 1980), the highest number of immigrant cygnets (70) might represent the total production of 30–40 pairs of breeding swans to September.

The numbers of swans drop in the New Year, presumably as many birds start returning to their breeding grounds. However, the number that remains on Radipole and the Fleet without attempting to breed is high and many of these are birds that were not born on either of these two waters. The points are discussed in more detail later.

With regard to long-term changes in numbers, we are fortunate in having autumn counts made by Estate employees since 1928 (Table 2). During this period there has been one major habitat change; Radipole Lake was converted in 1926 from an estuary to a lake by the building of a causeway and sluice. The northern end has been reduced in size especially on the west where a considerable area has become an island between two arms of the River Wey while further parts are now overgrown with reeds. An area at the south end was filled in and made into a car park in the 1960s. Probably as a result of this, the numbers on Radipole have declined. However, this re-

Table 2. Autumn counts of the number of swans on the Fleet and Radipole Lake, 1928 to 1980.

Year	Count	Year	Count
1928	1,551	1956	666
29	1,581	57	659
30	—	58	789
31	1,471	59	845
32	1,515	60	896
33	950	61	1,024
34	671	62	1,123
35	767	63	905
36	786	64	556
37	807	65	667
1938	810	1966	598
39	705	67	741
40	654	68	511
41	583	69	766
42	530	70	785
43	445	71	706
44	825*	72	771
45	500	73	645
46	489	74	803
47	399	75	824
1948	432	1976	801
49	643	77	711
50	700	78	882
51	931	79	906
52	1,037	80	940
53	1,167		
54	1,005		
55	815		

* November count

duction in the size of the habitat cannot be the whole explanation of changes in the population. A photograph in the *Daily Mirror* for 26th May 1934 shows a much larger flock of birds than we have ever seen and the caption says that there were then 'over 300 birds at Radipole Lake and the keeper hopes 200 cygnets will be raised this year'. Although the counts for this area (Table 2) suggest these hopes to have been somewhat over-optimistic, there is no doubt that the Radipole swan population is now but a shadow of its former self.

The 1962–63 winter was possibly the hardest in southern Britain for some 200 years and there was an obvious decline in swan numbers at that time. In March 1964 at least 100 swans died on the Fleet from an unknown cause, possibly disease linked with food shortage. Following the drought of summer 1976 which is believed to have reduced the growth of *Zostera* and *Ruppia* in the Fleet, an unusually high number of ringed birds were found dead on the Fleet and the numbers dropped over the winter of 1976–77. Nevertheless, there has been a gradual increase in the population during the period of our observations. The reasons for this are not totally clear.

Table 3 shows the numbers of breeding pairs at Radipole and Abbotsbury. The numbers breeding at Radipole dropped sharply between 1969 and 1972 and have since remained fairly static. However, the number of breeding pairs at Abbotsbury has gone up very markedly. The actual increase might be slightly less than that shown because in the early years we made counts at about monthly intervals whereas in the last two years daily observations have been made by R. Dalley. A few birds lay only one or two eggs and may then give up (Table 5); these short-lived nests are more likely to be missed by the former method than the latter. Nevertheless, the numbers of nesting pairs has gone up more sharply than the total population.

Table 4 shows the number of breeding birds which are known to have been born at Abbotsbury (either ringed as cygnets or having web-nicks). In addition, we know the place of birth of a small number of the other birds breeding at Abbotsbury. Since we have ringed almost all the cygnets at Radipole since 1968 any unmarked Radipole-born birds breeding at Abbotsbury would have been about 9 years old or older at the time when we started to catch the adults (1977). In view of the relatively small number of younger Radipole-born birds breeding at Abbotsbury, it is unlikely that there are many of these older ones. Similarly it is unlikely that there are many Abbotsbury-bred, but un-nicked, birds breeding at Abbotsbury. We believe that these potential sources of error are unlikely to be serious. We conclude that some 25% of the birds breeding at Abbotsbury were raised outside our study area.

Breeding season and clutch-size

Because our visits have only been made at roughtly monthly intervals, we do not have accurate laying dates for most of the clutches. Indeed, since there has been a certain amount of egg-stealing at Radipole, our data on clutch-size must also be considered open to error. However, since 1976 observations by D. Ireland at Radipole and since 1979 by R. Dalley at Abbotsbury have enabled us to obtain very much more accurate data for the two sites. The latter are presented in Table 5.

The data for breeding seasons and clutch-size at Radipole are not substantially different from other published data for southern and central Britain. However, at Abbotsbury there are some differences in both these features. The Abbotsbury nests are, from time to time, seriously affected by the high spring tides in April. Usually at this stage, most birds are only taking up nest-sites and building up the nests but in some years the first few may have started to lay; these lose their clutches and have to start again. Such flooding therefore delays the start of the breeding season, but only in an early year such as 1980. In a late year such as 1979 no birds have laid by the date of the high tides. Thus, breeding takes place at Abbotsbury, on average, a little later than at Radipole and elsewhere. There may also be some other factors which delay laying at Abbotsbury since the birds there never seem to attempt laying as early as the earliest breeders elsewhere.

Clutch-size at Abbotsbury is smaller than reported for other areas. The means of 1979 and 1980 are 5·07 and 4·62 respectively. These figures contain a number of very small clutches which, since they are sometimes quickly deserted, might not be included in other studies where less frequent visits are made. Nonetheless, if all the clutches of one and two eggs are excluded the means for the two years are still only 5·35 and 5·19 respectively. Seasonal

declines in clutch size have been recorded elsewhere and are apparent in both years for which data are presented here. Very many more of the clutches of six or more eggs were started before the middle of the laying period than later on, and very many more of the clutches of four or fewer eggs were started after that point than before it.

Table 3(a). Abbotsbury breeding record, 1969–1980.

Year	No. of nest with eggs	No. of young put into pens	No. of young released from pens	No. of young alive on Fleet*
1969	19	56	not known	8 (Aug)
1970	18	60	49	2
1971	25	72	45	
1972	32	72	c.33	24 (June)
1973	32	75	c.67	2 (June)
1974	33	82	78	5
1975	46	97	90	29 (June)
1976	53	c.104	104	2
1977	32	71	70	12
1978	57	103	102	4
1979	64	98	87	16
1980	100	109	89	12

* in September unless otherwise stated
Note. In 1979 and 1980 R. Dalley made more detailed observations and recorded 279 eggs (from 55 pairs) and 420 eggs (from 91 pairs) respectively.

Table 3(b). Radipole breeding record, 1969–1980.

	No. of pairs	No. of pairs laying	No. of eggs laid	No. of eggs hatched†	No. of young fledged
1969	35+	29	141	68–99	c.38
1970	30	23	121	51–67	37+
1971	24	18	81	50–69	19
1972	19	19	79	60–68	15
1973	19	15	68	41	9
1974	19	17	95	46–60	2
1975	21	14	68	26	10
1976	19	19	89	12	10
1977	20	18	83	23	8
1978	19	19*	107	32	7
1979	15	15	70	12	11
1980	19	17	89	43	17

* Four pairs relayed after losing their 1st clutches in a flood.
† In the years 1969–74 our visits were not frequent enough for us to be certain of the exact number of eggs hatching.

Note: Information for 1977 and later years is based on more detailed observations by D. Ireland.

Table 4. Numbers of different breeding swans bearing Abbotsbury web-nicks at Abbotsbury and Radipole, 1969–1980.

	Web-marked	Not web-marked	Not known
Abbotsbury	159	52	9
Radipole	6	37	91

Table 5. Clutch size at Abbotsbury in relation to laying date, 1979 and 1980, in 5-day periods.

1979 Clutch size	Date of 1st egg: April 1–5	6–10	11–15	16–20	21–25	26–30	May 1–5	6–10	Total
8				3	1				4
7			1	5	1				7
6				2	4	2			8
5				2	7	2			11
4				2	2	3			7
3					3	1	3		7
2					2				2
1						1	1		2
Total			1	14	20	9	4		48

1980 Clutch size	Date of 1st egg: April 1–5	6–10	11–15	16–20	21–25	26–30	May 1–5	6–10	Total
9			1						1
8		1							1
7	3	2	2	1					8
6	1	7	12	4	1	1			26
5	1	3	4	6	1	1			16
4			3	9	1				13
3		1	1	2		1	1	1	7
2		1	1	2		1		1	6
1			3	2	3				8
Total	5	15	27	26	6	4	1	2	86

Survival rates

We have measured the survival rates in a number of ways, but mainly by identifying the birds by their Darvic rings and assuming those that are no longer present have probably died. Since we know that a few of the younger birds have left the study area, the figures presented here are minimum estimates. Adult survival rates are probably very near to the true figure since adults do not usually move away from an area once they have started to breed. However, we do have a number of birds which have bred one year and are known to have been alive the following year, but were not breeding. Ensuring that these birds were located in the large flock at Abbotsbury has been a slight problem.

A more serious problem has been the identification of all the cygnets ringed in previous years. The large flock of non-breeders at Abbotsbury is never all out of the water together, so we have not been sure whether we were succeeding in seeing all the ringed birds that were alive or whether there were some that were avoiding being recorded by staying on the water. However in August 1980 we carried out a large round-up at Abbotsbury and caught 831 swans, missing a maximum of 18 (some of which were pairs with small cygnets which were intentionally left out of the round-up for fear of injury to the latter; the identity of the ringed parents was known). We also have a complete record of all birds present at Radipole Lake at the same date. It is unlikely that more than 10–15 ringed birds in the whole of the Radipole/Abbotsbury population were missed. In view of this, our analyses that follow make the assumption that the numbers of each age class correctly reflect the numbers still alive.

Table 6 gives the annual survival rates for the adults at Abbotsbury and Radipole. There are fewer pairs per year for the former site, but a much longer run of years. These survival rates are higher than those reported for adult breeding swans in other areas (Perrins & Reynolds 1967; Bacon 1980; Coleman & Minton 1980). It is perhaps worth nothing that we have had one bird (ringed at Weymouth in September 1961 as an adult) which has reached at least the age of 21, an unusually ancient Mute Swan for central or southern Britain.

Table 7 sets out the number of cygnets

Table 6(a). Survival of breeding adults at Abbotsbury.

Year ringed	Years since year of ringing									
	No.	1	2	3	4	5	6	7	8	9
1970	2	2	1	1	1	1	1	1		
1971	6	6	6	6	6	4	4	3	2	2
1972										
1973										
1974	3	3	3	3	1	1	1			
1975	4	4	4	3	3	3				
1976	74	72	68	58	55					
1977	15	15	15	14						
1978	20	20	19							
1979	15	15								
Total	139	137	116	85	66	9	6	4	2	2
Survival (%)		98·6	96·1	87·6	92·9					
Mean		93·6%								

Table 6(b). Survival of breeding adults at Radipole.

Year ringed	Years since year of ringing										
	No.	1	2	3	4	5	6	7	8	9	10
1969	29	25	22	18	14	9	7	6	2	2	1
1970	5	5	5	5	2	1	1				
1971	9	9	9	9	7	7	6	6	5	5	
1972	4	4	4	4	4	4	4	3	3		
1973	2	2	2	2	2						
1974	4	4	4	4	4	4	4				
1975	4	4	4	4	4	3					
1976	4	4	4	3	2						
1977	5	5	5	4							
1978	1	1	1								
1979	0										
Total	67	63	60	53	39	28	22	15	10	7	1
Survival (%)		94·0	96·8	79·6	75·7	88·0	83·3				
Mean		86·2%									

ringed each year at Abbotsbury, and the totals known to be alive in each succeeding year. No young were ringed in 1972 or 1973. The mean annual survival rate and the 1st year survival rate for each cohort are given, together with overall survival rates for all the birds marked.

The overall survival rates of the cygnets, though not all the first year rates, are markedly higher than comparable figures for swans elsewhere in Britain (Perrins & Reynolds 1967; Bacon 1980; Coleman & Minton 1980). Furthermore the birds attain an adult level of survival as early as their second year, whereas other studies have shown that this does not normally happen until at least the third year.

Individual survival rates from the different cohorts are quite variable. In some years, notably 1970, 1977 and 1979, first year mortality was no greater than among adults—a most surprising result. In other years mortality was much greater. The survival of the 1976 cygnets, for example, was almost certainly adversely affected by the drought of that year which resulted in a poor growth of aquatic vegetation and consequent food shortage through the winter. The 1978 cygnets appeared to have been badly affected by the unusually cold weather of winter 1978–79 and spring 1979, though this weather does not seem to have had any such effect on older birds. Samples in some of the earlier years are rather small but lower survival rates may be linked to the relatively poor condition of the young when released in some of those years.

We have weighed the cygnets on their release in recent years and the mean weights of these are shown in Table 8.

Table 7. Survival of cygnets ringed each September at Abbotsbury.

Year ringed	Years since ringing											Mean annual survival	1st year survival
	No.	1	2	3	4	5	6	7	8	9	10		
1970	49	42	36	31	29	27	23	18	15	12	11	86·1	85·7
1971	32	19	17	17	15	15	14	12	10	10		87·9	59·4
1974	33	26	26	22	22	16	15					87·7	78·8
1975	27	18	17	12	11	9						80·4	66·7
1976	106	40	36	31	28							71·7	37·7
1977	82	74	67	65								93·0	90·2
1978	103	49	45									66·1	47·6
1979	103	95										92·2	92·2
Totals	535	363	244	178	105	67	52	30	25	22	11		
Survival (%)		67·9	91·0	89·4	92·9	87·0							
Mean	86·3%												

Table 8. Mean weight of cygnets on release in September.

Year	No	Mean weight (kg)	Range
1976	106	6·3	3·8–9·2
1977	81	6·0	3·5–9·4
1978	103	4·7	3·0–7·3
1979	103	6·5	3·0–8·2
1980	101	7·5	4·5–10·5

There is no obvious correlation between the mean weight of the young in September and how well the young subsequently survive except that, as already mentioned, the years with very light young seem to be followed by low survival.

Table 9 shows the survival in relation to weight within years; there is a clear correlation. There is some slight evidence that the weights of young may vary in relation to the numbers of young in pens.

The breeding birds

Because the breeding birds at Abbotsbury have only been marked in relatively recent years, we have less information on this section of the population than we would like. However, we are in the position to make the following observations.

1. Age at first breeding. We have 24 records of the age of first breeding for birds raised at Radipole (Table 10). There seems to be no clear indication of a difference between the sexes. However, for both the 1976 cohorts (which were four and three years old respectively in 1980), more females have started to breed than males (12♀; 6♂ for 1976, 14♀; 8♂ for 1977). Females have been reported to start breeding at an earlier age than males elsewhere (Minton 1968).
2. Regularity of breeding. Tables 11a and 11b show the number and percentage of breeding birds at Abbotsbury and at Radipole which are known, with reasonable certainty, not to have attempted to breed in years subsequent to a year in which they did breed. Overall, this applies to 46 of 246 Abbotsbury birds (18·7%) and to 61 of 245 Radipole birds (24·9%). Although we do not know of comparable data for other populations of swans, these data suggest that a significant proportion of the swans which have achieved breeding status may subsequently not breed in a particular year. On the available evidence, Radipole swans have a lower probability of nesting than those at Abbotsbury.
3. Origins of breeding birds. As stated earlier (see Table 4), we can distinguish birds which were raised at Abbotsbury (web-nicked). There is no evidence that the 'immigrant' birds are less successful than the resident ones; the clutch-size, breeding frequency and survival are closely similar for the two groups.

Table 10. Age of first breeding at Radipole.

	Age in years								
	2	3	4	5	6	7	8	9	10
Males		3	4	1	2	1			1
Females		2	5	2	1	2			

Weights

We have a series of weights of fully grown and breeding swans from Abbotsbury (Table 12). The swans are consistently lighter at Abbotsbury than they are elsewhere (Reynolds 1972). We do not know the reason for this, but it is interesting to note that Andersen Harild (in press, a) shows that swans feeding on *Zostera* as their main diet may be lighter than those which depend on other sources of food. Although the Abbotsbury swans are fed small quantities of grain each day, not all take advantage of it and even for those that do, *Zostera* and other plants form the major part of their total diet,

Table 9. Survival of cygnets to one year by weight on release in September.

	1976		1977		1978		1979	
Weight	No.	%	No.	%	No.	%	No.	%
Heavy	33	54·5	27	96·3	30	73·3	37	94·6
Middle	41	43·9	25	92·0	40	50·0	33	93·9
Light	32	12·5	29	86·2	33	21·2	33	87·9

Table 11(a). Abbotsbury breeders—breeding status in following year.

Year of breeding	BREEDING with same mate No.	%	with different mate original alive	original dead	Mate dead	NOT BREEDING Mate alive non-breeding No.	%	breeding with another swan	Total
1974	2	*50*				2	*50*		4
1975	2	*50*	2						4
1976	10	*52*			1	13	*54*		24
1977	28	*76*	1	1	2	4	*11*	1	37
1978	56	*74*	1	2	3	13	*17*	1	76
1979	90	*89*	4	1		44	*4*	2	101
Total	188		8	4	6	36		4	246

Table 11(b). Radipole breeders—breeding status in following year.

Year of breeding	BREEDING with same mate No.	%	with different mate original alive	original dead	Mate dead	NOT BREEDING Mate alive non-breeding No.	%	breeding with another swan	Total
1969	20	*67*		1	3	6	*20*		30
1970	22	*69*			1	9	*28*		32
1971	12	*48*	1	1	3	7	*28*	1	25
1972	10	*63*			3	3	*19*		16
1973	16	*89*		1	1				18
1974	10	*67*			2	3	*20*		15
1975	10	*71*	1		1	1	*7*	1	14
1976	10	*71*	2		2				14
1977	22	*85*		1	1	2	*8*		26
1978	18	*60*	1	4	2	5	*17*		30
1979	18	*72*	1	2	1	2	*8*	1	25
Total	168		6	10	20	38		3	245

Table 12. Weights of adult swans.

	No.	Mean weight (kg)	Range
Breeding birds in May/June			
Male	3	10·6	10·0–11·3
Female	2	6·2	5·6–6·7
Breeding birds caught in August (known to have lost broods)			
Male	4	10·6	9·0–12·2
Female	11	7·6	6·4–9·7
Breeding birds in pens in September			
Male	9	12·8	10·6–15·1
Female	6	9·3	8·5–10·5
Non-breeding birds in August			
Male	70	10·1	7·5–13·3
Female	71	8·0	5·0–10·7

Discussion

One might argue that the situation at Abbotsbury is so unnatural that it is of little general interest. We suggest that this is an over-simplification. Although production of young is obviously greatly affected by the very unusual management techniques, once the young have been released in September, the birds fend for themselves in an entirely natural, if unusual, situation. It is therefore valid to make comparisons between these birds and swans living elsewhere in Britain, and also in Denmark, where colonial breeding is quite common.

Other British populations

There are three main areas where detailed studies have been carried out on territorial Mute Swans: (i) the Oxford area (Perrins & Reynolds 1967; Bacon 1980); (ii) the Birmingham area (Minton 1968; Coleman & Minton 1980); and (iii) the Stratford-on-Avon area (Hardman & Cooper 1980). Many of their findings are closely similar. There has been a slow decline in the number of non-breeding birds in all three areas, particularly noticeable with the loss of most of the urban flocks, while the number of breeding pairs has held up better, though also decreased. The principal factors which are thought to have brought about the decline, mortality from lead poisoning from fishing weights (Simpson *et al.* 1979; Birkhead 1981), and increased disturbance and habitat degradation through boating and dredging, have not applied at Abbotsbury.

Laying dates of these inland territorial swans, even those much further north, are consistently earlier than at Abbotsbury, though there is little difference from the Radipole birds. Mean clutch size among the territorial swans is as much as 1·5 or even 2·0 eggs greater. Losses of downy young cygnets are always considerable on inland sites, comparable to those at Radipole.

It is in the subsequent survival of the swans that the most marked differences between the studies of territorial swans and those at Abbotsbury occur. The survival of the young birds from September to the end of their first year of life is not so different overall, 67·9% for Abbotsbury birds, compared to 65–70% for birds on the Thames (Perrins & Reynolds 1967; Bacon 1980), and 41·4% in the Birmingham area (Coleman & Minton 1980). The range of survival rates for different cohorts at Abbotsbury seems very great, however, (37·7–92·2%) and it seems highly unlikely that survivals in excess of 90% are often achieved by birds at these other sites.

The survival in the second and third years of life among Abbotsbury swans is virtually the same as that for adults (c.90%). This is in marked contrast to the figures from other areas. In the Birmingham area, the survival in the second year is 67·7% and in the third 69·3%, and it is not until the fourth year that it approaches the adult survival rate of around 80% (Coleman & Minton 1980). Similarly the swans in the Oxford area achieve survival rates of c.70% in their second year and c.75% in their third year, again attaining adult rates of c.80% in their fourth year (Bacon 1980).

There is one other study taking place in Britain with which comparison can be made, that on the isolated population of Mute Swans in the Outer Hebrides. It has been taking place for only a short time, so much less is known especially about survival rates beyond the first year. However the population shows some similarities with that at Abbotsbury; production of young is low and there is a high proportion of non-breeders (Spray, in press).

Continental populations

The most intensive studies are those of Andersen-Harild (in press, a, b); for our purposes, they are certainly amongst the most important since they compare 'normal' populations with those that nest colonially. As at Abbotsbury, the latter are on salt water, though in these Danish populations some are on the sea rather than on brackish water sites as at Abbotsbury.

In spite of the artificial nature of the Abbotsbury colony and its management, the breeding shows certain similarity with that in the Danish colonies which breed late and have low productivity (raising on average some 0·9 young per pair compared with 2·6 for pairs which nest solitarily).

Another feature of the Danish colonial birds which is also found in the Abbotsbury population is a very variable first year survival. In both studies, for first year birds in some years, the survival rate may be as high as 90% or more while in others they may be very low. One year in a Danish area only some 5% of the young survived their first winter. Mortality at Abbotsbury

has never been as high as this. The same is true for the other age classes; the mortality of Abbotsbury birds is lower. This is not at all surprising since the Danish birds' three major causes of death, severe winter weather, oiling and flying into overhead wires, do not have any present importance at Abbotsbury.

Age structure and balance of numbers

Perhaps the most surprising feature of this and the other studies quoted above is the great variation in the patterns of productivity and survival which are found in the different populations, yet they all (with the recent exception of those in lowland Britain) maintain their numbers.

The colonial populations have low productivity (which at Abbotsbury is improved because of the way in which some of the young are looked after artificially). It is also low in the Hebrides because of the limited number of good breeding sites (Spray, in press). Noneless, the young that are raised often have very good survival. The same is true for the older birds at Abbotsbury and probably in the Hebrides (the very large proportion of non-breeders in the population there makes this a safe inference).

In comparison, the lowland British populations tend to hatch and raise more young per pair, but these and the immature and adult birds never achieve the high survival rates shown by the colonial birds (and probably those in the Hebrides).

Some of the comparisons are difficult to make in precise quantitative terms. Because of the high numbers of immigrants, it is difficult to give an accurate figure for the proportion of non-breeders, from whom the future breeders will be drawn. At Abbotsbury, the two extremes are 1969 (when 19 pairs bred and there were 275 non-breeders) and 1980 (when 100 pairs bred and there were 294 non-breeders) (Table 3a). In both these cases, the non-breeding element is far larger than 'needed' to maintain the population. The population should therefore be increasing which is, in fact, the case.

Because the number of breeding pairs at Abbotsbury has varied five-fold, whereas the young raised have varied only two-fold, the number of cygnets raised (by the population as a whole) to autumn is very variable. Survival from autumn to the following summer is also very variable (43–93%, Table 7). The combination of these two features results in a highly variable production, much more so than in other populations.

A very low number of one-year old birds may result, but this is more than counterbalanced by the very high survival figures for birds which survive their first winter. We can see from the data in Table 7 the number of birds from any cohort which reach the breeding age of four in any year. This has ranged between 17 and 65. Even the lowest number is greater than the number of adults which usually die in 100 pairs (14 if survival is 93%). In most years, the numbers of birds which survive greatly exceeds that needed to replace the breeding birds which die.

Since the population at Abbotsbury is currently increasing, one might speculate on what will eventually happen. There have been occasions in the past when the birds have died in large numbers, apparently because they have eaten out the *Zostera*. It is interesting to note (Table 2) that numbers have never been as high as they were in the early years of the counts, though they have twice reached about 1,100–1,200 birds, the current level. On both previous occasions the numbers then declined and stayed down for some years. It is tempting to speculate that this may represent the 'carrying capacity' of the Fleet.

In conclusion, we would suggest that these studies of Mute Swans in several different habitats have shed an interesting light on how varied patterns of survival can still result in populations being maintained.

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Summary

The Mute Swan *Cygnus olor* population of the Fleet and Radipole Lake, Dorset, have been studied since 1968. The majority of the breeding pairs are in a colony at Abbotsbury on the Fleet. A proportion of their cygnets are reared artificially; few others survive. Regular counts show an influx of birds coming to moult and to winter; their origin is not yet known. Long-term counts show only moderate fluctuations in numbers, the peak having varied from 733 to 1,238 in the course of the study, while the number of breeding pairs has varied from 18–100 at Abbotsbury, and 15–35 at Radipole Lake. The breeding season starts later and the clutch size averages smaller than the Mute Swans elsewhere in southern Britain.

Survival of adult birds is higher than elsewhere in Britain, and that of the reared cygnets can be very high. The latter show a correlation between weight and survival.

Females start to breed earlier than males, but significant proportions of both sexes do not breed every year despite having achieved breeding status.

Comparisons are drawn with colonially breeding swans in Denmark and with populations of territorial birds elsewhere in Britain.

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