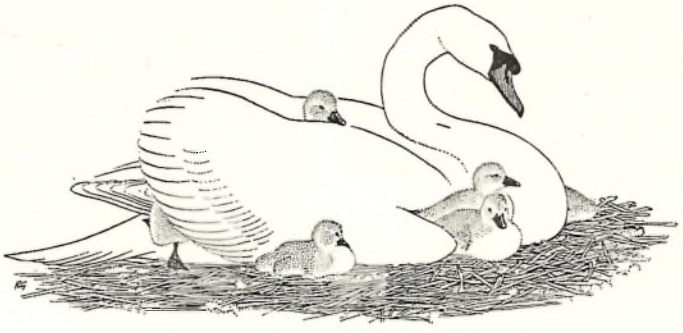

A preliminary study of the Mute Swan, *Cygnus olor*

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Summary

Results of a preliminary study of the Mute Swan in the Oxford area 1960-66. Distribution and movements are discussed: relatively few birds seem to travel any distance during their life and those that do are mostly immature. Mean clutch-size is about six, close to the national average; mortality is about 50% between hatching and fledging in September, and brood-size in September is about three for those pairs with young or two if the unsuccessful breeders are included. About one-third of the remaining young die within nine months October-June. Thereafter mortality is about 33 — 25% per annum for the next two-three years, dropping to 18% for breeding adults (birds most commonly start breeding at three or four). Highest losses appear to occur in late winter and early spring. Life-table data suggest that the Mute Swan is maintaining its numbers within the study area, but there is evidence that there are more suitable nesting sites than there are pairs to occupy them.

Introduction

This paper is an interim report of a spare-time study of the Mute Swans *Cygnus olor* of the Oxford area. This species has been surprisingly little studied in Britain, especially when one considers that it possesses several advantages over most species for population studies. Amongst these, the most important are its conspicuousness and ease of capture. It is possible to get more accurate counts of this species than almost any other bird and, perhaps uniquely, it is possible to measure the non-breeding population. In addition, in central and southern Britain a higher proportion of the swans than of any other species are caught and ringed. The advantage of this is that many of the swans that have left our study area have been recaptured by other ringers. In addition, some 20% of the birds which we have ringed have been recovered by members of the public who have found them dead or injured; this is an exceptionally high recovery rate.

The study area

The area which we have covered is centred on Oxford; roughly, it is central and west Oxfordshire and the Thames valley of north Berkshire (see Figure 1). Within this area there are some 60 miles of the river Thames, plus the tributaries Windrush, Evenlode, Cherwell-Ray and Thame. All these and the Oxford Union Canal (which runs parallel to the Cherwell for much of its length) pass through Oxfordshire. North Berkshire is comparatively poor in waters, containing only a few small brooks, gravel pits and lakes which harbour swans; in these also, Oxfordshire is better supplied.

Methods and background

The study started in early 1960. Since then the coverage of the non-breeding flocks and the breeding pairs in and around Oxford and Abingdon has been fairly consistent. The coverage of the rest of the area has been more limited, consisting in the main of summer visits to

look for breeding pairs and to find birds ringed in the towns that had moved out into the country to breed. We have not even covered the whole area during each summer and have relied on other records to augment our own. In recent summers, however, more of the area has been covered and nearly all of the known breeding sites have been visited. Most of the sites were visited only once a year, the commonest time being when the birds were incubating, since this is the time when most swans are easiest to catch. We have, therefore, little information on the breeding season and our clutch-size records are minimal. From 1964 we have some information on breeding success for broods which we were able to follow after hatching (see also Reynolds 1965).

Unringed swans have been caught and ringed whenever possible; each bird has been given a numbered metal ring and, with very few exceptions, two coloured rings, the combination of the three rings being unique to any particular bird. Thereafter, the birds have not normally been recaptured unless the coloured rings were becoming difficult to read or the birds were nesting; identification can readily be made by the colour combination.

The young were mostly ringed when

Figure 1. An outline map of Oxfordshire and Berkshire showing the main waterways and the three towns where large non-breeding herds of Mute Swans occur. The dotted line shows the approximate demarcation of the study area.

they came into the non-breeding flocks during winter and hence were not of known parentage, though since 1964 an increasing proportion of the cygnets have been ringed before the family parties split up. The main age groups used were cygnet (or first year), immature and adult. A cygnet's year of birth can be told for the whole of its first year and sometimes for part of its second; from being a downy cygnet it moults to a dark brown bird and then gradually replaces the brown feathers with white throughout the winter and spring. In some cases there are still some brown feathers, especially on the rump, during the next autumn and winter. White birds with lead-coloured beaks are normally birds in their second year of life, though they may occasionally be older; it is these that form the majority of our age class " immature "; birds which have acquired the red bill are normally in the third or later year and we cannot determine their age. Over the years progressively more and more of the birds have been ringed in their first year so that errors in ageing immatures are not likely to be serious.

Young birds were not usually sexed, but the sexes of the breeding birds were recorded. This was usually easy to do when both birds were present at the nest since the male tends to be the larger of the two and to have the larger knob on the bill. However, we also used behavioural differences which, we believe, are reliable.

The Annual Cycle

Mute Swans nest in early spring, laying occasionally beginning in late March, and many of the young are full-grown by late August, by which time their parents have usually moulted. Some young can fly by late September (Heinroth 1924-8 gives 4½ months for the fledging period), after which they may come into the non-breeding flocks (mainly in Oxford and Abingdon); sometimes they are accompanied by their parents. Many of the young, however, appear to be forced to leave their birth-place by the increasing territorial aggressiveness of their parents, and the largest influxes into the non-breeding flocks may occur in January or early February, but there is considerable variation from year to year.

These cygnets may move from one area to another, but commonly they remain in the flocks during the summer, moult and spend the next winter there also. They may then leave in the spring of their second year, possibly to search for a breeding area, though they do not normally breed at the age of two. Some may settle as non-breeding birds in territories, but the majority seem to return to the flocks for at least some of the time and many two-year-olds moult there in the summer. While the majority of birds in the flocks are one and two years old, there are older birds among them and there was one bird present in the Oxford flock up to the age of seven years without apparently ever attempting to breed. The numbers of older birds in the flocks may be augmented during mid-summer by failed breeders which come into the flocks to moult.

The breeding territories are situated along the Thames, the smaller rivers and the still waters (mostly gravel pits) of the area, usually where there is sufficient shallow water for the young to be able to get food (though the parents may bring the food to the surface for them). The territories are usually well-spaced, and though in Oxford there have been nests within about 100 yards of one another, the average distance between nests on the rivers is about 1½ — 2 miles. The breeding pairs often remain in or around the breeding territory throughout the year, though some may visit the flocks. The most common time for them to move is during a cold spell when the still waters freeze over.

Movements

Figure 2 shows the recoveries by month of those swans killed by flying into overhead wires. A few of these birds are known to have collided with the wires during darkness. We believe that the peaks in autumn and in early spring are genuine reflections of greater amounts of movement at these times.

Figure 2 also shows the times at which all other swans have been reported as being found dead, except those which died as a result of oiling. Causes of death for only some 40% of these birds were given by the finder and so some of these birds also may have been killed in collisions with overhead wires. However, since it is usually obvious if a bird has flown into wires, we think it unlikely that many of these swans will have died in this way. There is some tendency for both groups of birds to have died in the same months. The reason for this correlation is not clear, but we suggest that the birds have died as a result of having had to move. Shortage of food, territorial

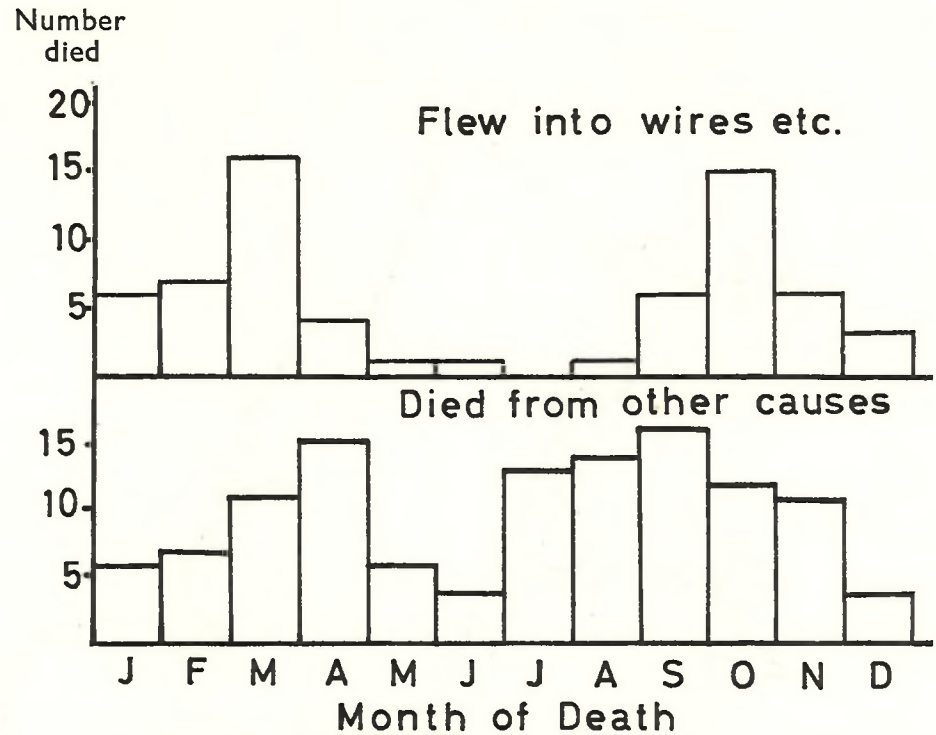

Figure 2. Monthly distribution of recorded deaths of Mute Swans in the Oxford study area. Deaths are divided into those birds which are known to have collided with an object in flight and all other causes (which were often not recorded by the finder of the bird). In both categories there is a tendency for there to be more deaths in spring and autumn than in summer and mid-winter. Deaths from oiling are not included.

aggressiveness of the parents, or the need to find a suitable nesting site may all make a bird leave the water it is on. It seems clear that moving is dangerous and therefore presumably birds move only when it becomes necessary to do so; presumably, on balance, those birds are more likely to survive if they move than if they do not. Ogilvie (1967) deals in detail with causes of death of ringed Mute Swans in Britain.

A number of birds are known to have left the study area and the places of recovery of these are shown in the map (Figure 3). A few of these have been recovered in more than one place. Four of the five recoveries at Barrow-in-Furness probably moved there as a party, since they were found there together. One of these had previously been trapped near Birmingham. It was taken from a group of locally colour-ringed birds which may well have included the others from Oxford. The catcher, however, was not at the time familiar with the colour code in use in the north Midlands and did not realise that any of the birds might be alien. At any rate the birds apparently arrived together and none were observed in Oxford after the one was recovered in Birmingham.

There is a large non-breeding flock at Reading, just outside our area. We have visited it from time to time since some of our birds, especially those from Abingdon, have gone there; this is a distance of about 18 miles in a straight line or 30 following the river. There is clearly some interchange with the Reading flock, but there seems to be relatively little movement between birds ringed in our area and the Henley flock, about 6—8 miles below Reading. Apart from six birds that have moved from Oxford to Reading, only 38 swans ringed in our area are known to have left. Ten of these were ringed during the hard weather in the first two months of 1963 and were probably wanderers then, since there was much movement due to most waters being frozen over at that time.

Figure 3. Long-distance movements of Mute Swans ringed in the Oxford study area. All recoveries of birds leaving the study area are shown, except some that have moved to Reading. It seems likely that the birds have avoided crossing the higher ground and have followed waterways. The Oxford Canal and River Cherwell head north to Banbury, the canal going on, or running near to, the river and canal systems of Birmingham and Coventry, and further north; the headwaters of the Cherwell run very close to those of the River Ouse which runs through Bedford and near to Cambridge.

Of the 38 birds 28 were only seen on the day of ringing and clearly must have left soon after. Including the six birds that went from Oxford to Reading, 41 out of 44 birds were ringed in their first year (21) or their second year (20). Of these 41 only two did not leave the area in or before their second spring. The remaining three of the 44 birds were older birds, two of which left immediately and the third within a month. No adult breeding bird of ours is known to have left the area. Hence we think that it is unusual for birds to leave our area entirely; this is supported by Ogilvie (1967) who has shown that the large majority of swans remain in the watershed within which they were ringed. Of those birds that do leave, it seems that it is exceptional for them to do so after they are two years old and we doubt that breeding birds ever normally do so. There is the further point that the places of recovery strongly suggest that the birds have left our area by following the river valleys rather than crossing the higher ground, the birds having followed the Thames or the Cherwell—Ouse complex.

Age of first breeding

We have relatively few certain records of birds breeding for the first time. For most of these there is little doubt that the age given in Table Ia is that at which breeding was first attempted. Even those that first bred at six years are unlikely to have attempted to breed before since they remained in the non-breeding flocks for most of the previous period. One of the birds that first bred at two laid a clutch of six eggs and raised four young; the other reared three.

It seems clear that 3 — 4 is the most common age at which breeding starts but, as mentioned earlier, some two-year-olds may establish a territory, though breeding is exceptional at this age. The figures in Table Ia will be slightly biassed in favour of birds breeding at an early age since not only have we more data on younger birds, but also it is harder to be certain that older birds have not attempted to breed in some of the earlier years. However, one 1959 cygnet had not attempted to breed by 1966, i.e., at 7 years. Table Ib gives the percentage of each age class that was known to be breeding or not breeding. This shows that, while 3—4 years is a common age to start breeding, a significant proportion of the birds do not start until later than this.

Eggs and young

As mentioned earlier, we have little information on the timing of the breeding season, beyond the fact that there is considerable variation in the time at which the clutches are started. Our few records tend to confirm that eggs are not normally laid daily, but at about 48-hour intervals. Repeat, small clutches are sometimes laid after the first clutch has been lost. Flooding is the most common cause of wide-spread losses and probably affects the earliest breeders most frequently.

Table I. Age of Oxford Mute Swans at first breeding.

(a) Numbers of birds which started to breed at known age.

	age in years					
	2	3	4	5	6	7
♀ *certainly breeding for first time*	2	13	7	1	1	
♂ „		9	5	2	2	
♀ *probably breeding for first time*		5	4	5	1	
♂ „		2	2			1

(b) Proportions of birds known to have been breeding in relation to age.

Note: Table Ib based on cygnets hatched in 1960-62 only.

Year	*% Breeding*	*% Not breeding*	*Uncertain, but probably did not breed*	*Total*
Third	10.5	54	35.5	76
Fourth	37	35	28	60
Fifth	53	35	12	34
Sixth	71	29	0	14

Clutch-size (which is a minimum figure since eggs may be lost or stolen, or, in a few cases, the clutches may not be complete at the time of our visit) is around 6.0 (Table II), agreeing with Eltringham 1963) and Campbell (1960) who gave figures of 6.0 and 5.9 respectively. There do not seem to be marked differences in clutch-size in relation to the age of the female.

Reynolds (1965) followed the survival of the cygnets in 18 broods of swans around Oxford in 1964, and calculated the death-rate in each week of life. This was much the highest (22%) in the second week of life. Dr. J. Kear (pers. com.) informs us that a brood of swans which she observed, and which, for some reason, could not be induced to feed, survived until they were 10—11 days old. Heinroth (1928) states that over 25% of the young Mute Swan's weight at hatching is made up from yolk sac; this is retained within the body cavity and Heinroth records that the young swans can live off this for several days without other food. Similar observations have been made by Marcstrom (1966) on Mallard *Anas platyrhynchos* ducklings. At hatching, some 13.5% of the young Mallard's weight is made up from the yolk sac and the ducklings can live off this for about a week without other food. It therefore looks as if newly hatched young of some species of waterfowl (including the swans) are able to survive for a considerable time in adverse conditions. Reynold's findings therefore make it seem likely that the high mortality he observed in the second week of life was due to starvation when the cygnets' internal food reserves ran out.

Reynolds (loc. cit.) further showed that approximately 50% of the hatched young survived until September (after which it became harder to follow the broods since they tended to split up). In 1964 the mean brood-size in September (of all pairs which hatched at least one young) was 3.1. The range of variation is shown in Table III alongside the data for 1965 and 1966; there is relatively little difference between years. It is more difficult to provide a figure for the number of young produced per pair including those that lost all their eggs, since we were not able to visit the areas frequently enough to distinguish all failed breeders from non-breeders. However, we estimate (assuming that most old pairs without young attempted to nest—which seems to be true) that about one third of the pairs lose all their eggs and do not replace them; if this is true then approximately 2.0 young are raised per pair to September.

Table II. Clutch-size of Mute Swans in the Oxford study area.

Clutch-size	*Number of clutches*		
	1964	1965	1966
1			1
2	1		2
3	3	2	7
4	1	4	5
5	3	2	7
6	5	3	11
7	7	3	9
8	3	1	10
9	2	1*	4
10	1*		1
11			1*
Number	26	16	60
Mean	6.2	5.5	6.0

Notes: 1. Excluding 3 clutches known to be repeats, one of 5 in 1964 and two of 4 in 1966, average 4.3.
2. There was a strong tendency for the clutches which were kept under observation throughout the laying period to be larger than those which we visited only once. Hence we suspect that many of the smaller clutches may have been robbed. The mean for clutches which were observed several times was 6.8.
3. The largest clutch in each year (marked *) were all laid by the same female. This bird was a breeding adult in 1960 and is of unknown age, She retained the same mate for the years 1963-66 inclusive, and is known to have raised to September: 6 young in 1963 (clutch-size unknown), 5 in 1964, 8 in 1965 and 8 again in 1966.

Table III. Brood-size of Mute Swans in the Oxford study area in September.

Brood-size	*No. broods 1964*	*No. broods 1965*	*No. broods 1966*
0	3	3	2
1	3	7	7
2	4	2	7
3	4	5	5
4	1	3	5
5	2	3	0
6	3	2	4
7	2	1	2
8	0	1	2
Mean	3.1	3.0	3.2

Survival in later life

We have estimated the survival of young birds after September by observing the birds which we ringed in the non-breeding flocks and noting the time at which they disappeared. An estimate based on such observations is open to several sources of error. When a bird disappears it may not have died, but may merely have moved outside the limits of our area. We have shown that we do not believe that such movement is on a very large scale but it is worth noting that there seem to be seasonal periods of movement (Figure 2). Also a bird might not have died for some time after a last sighting of it, but because of a gap in our observations we did not see it during the remaining portion of its life. However, biasses due to uneven observations on our part should average out over a long period and produce an estimate of only a slightly shorter expectancy of life.

A further difficulty arises in the estimation of mortality of ringed young swans. A young bird is identifiable as such throughout the whole of its first year of life (sometimes even longer) and may be ringed at any time during this period. It is not therefore valid to lump all the data for birds of one year when analysing their survival since, for example, a bird ringed in September is less like to survive to the following June than is a bird ringed only in March. In an attempt to overcome this difficulty we have made our analyses in quarter-year periods and scored the number of birds known to have been alive in each period against those which were not seen again after that period. For example, if 10 birds were ringed in the quarter October-December and five of these were seen during the quarter January to March, when another ten birds were ringed, the survival for January to March would be based on how many of the 15 birds known to be alive then were seen again; if five more were not seen after March then the survival would have been $10/15 = 67\%$. Four such survival figures were obtained for each year and the annual survival was calculated as the product of these.

The calculated survival figures for birds ringed in their first year are shown in Table IV. Since few cygnets were ringed in the quarter July-September the figure of 50% (obtained from observations on the broods—see above) has been used for this period. Also shown in Table IV are estimates, calculated similarly, for birds ringed as "Immature" (nearly all of which are probably in their second year of life). Several points may be noted. First the survival figures are higher for these birds than for those ringed as cygnets, even when the same year classes are compared. The reasons for this are not clear. Even if a few older birds were included in each year class there is no evidence (from this table) that this would result in a higher survival-rate.

Survival of the Immature birds is markedly lower in their second spring—the time when it has been suggested that the birds start to look for breeding sites. However, no such marked decrease in survival is noted for the cygnets when they are two years old. We think that this is probably because some birds ringed as immature have been wanderers when caught. This may have been particularly true of the large numbers of birds caught in the cold periods of 1962 and 1963, especially the latter. Although we have no reason to believe that our breeding birds suffered unusually high mortality during these periods (see below) we lost

TABLE IV. Estimates of mortality of young Mute Swans in the Oxford study area.
(m = mortality; s = survival; $\hat{s}$ = calculated survival)

Quarter-year periods	*Ringed in first year*					*Ringed as immature*				
	Known alive in quarter	*Last seen in quarter*	*% m*	*% s*	*$\hat{s}$(%)*	*Known alive in quarter*	*Last seen in quarter*	*% m*	*% s*	*$\hat{s}$(%)*
1st year										
Jul-Sep			50*	50*						
Oct-Dec	129	17	13.2	86.8						
Jan-Mar	255	28	11.0	89.0						
Apr-Jun	355	43	12.1	87.9						
					33.7*					
2nd year										
Jul-Sep	348	29	8.3	91.7		81	9	11.1	88.9	
Oct-Dec	327	29	8.9	91.1		149	18	12.1	87.9	
Jan-Mar	317	46	14.5	85.5		255	57	22.4	77.6	
Apr-Jun	271	26	9.6	90.4		251	33	13.1	86.9	
					64.6					52.7
3rd year										
Jul-Sep	189	20	10.6	89.4		218	15	6.9	93.1	
Oct-Dec	169	6	3.6	96.4		203	12	5.9	94.1	
Jan-Mar	163	19	11.7	88.3		191	18	9.4	90.6	
Apr-Jun	144	15	10.4	89.6		166	10	6.0	94.0	
					68.3					74.6
4th year										
Jul-Sep	86	7	8.1	91.9		159	7	4.5	95.5	
Oct-Dec	79	4	5.1	94.9		149	6	4.0	96.0	
Jan-Mar	75	9	12.0	88.0		143	16	11.2	88.8	
Apr-Jun	66	8	12.1	87.9		116	15	12.9	87.1	
					67.4					70.5
5th year										
Jul-Sep						101	5	4.9	95.1	
Oct-Dec						94	5	5.3	94.7	
Jan-Mar						89	9	10.1	89.9	
Apr-Jun						60	3	5.0	95.0	
										76.8
6th year										
Jul-Sep						57	4	7.0	93.0	
Oct-Dec						53	4	7.5	94.4	
Jan-Mar						49	3	6.1	93.9	
Apr-Jun						35	3	8.6	91.4	
										75.3

* The 50% survival for cygnets in late summer is not based on observations of ringed birds, but on survival of cygnets within broods (see p. 80). The calculated annual survival for the last three quarters only of the first year = 67.9%.

Notes. 1. The January-March mortality of 22.4% for Immatures in their second year is probably biassed by high mortality during the hard winter of 1963. Because most waters froze over during this period abnormally large numbers were ringed in Oxford during this time and Ogilvie (1967) has shown that there were heavy losses during that winter.

2. The small number of birds that were seen alive outside our area have been included in this table and have been scored as having died in the quarter in which they were last reported.

large numbers of immature birds during this time—whether due to movement or death we cannot say but it will be remembered that a quarter of all the birds that moved out of our area were ringed during the cold spell in 1963. Boyd and Ogilvie (1964) showed a high mortality during these winters. A reason for suspecting that not all the disappearance in spring is due to birds moving out of our area is that there is a tendency for the quarterly losses (Table IV) to be greatest during the January-March (and sometimes April-June) periods of the year, even for birds older than two (see also Ogilvie 1967). Since it is unlikely that the losses of the older birds are due to movements out of the area, it seems probable that there are higher death-rates during these times. Not only is this the time of year when natural food is likely to be scarcest, it is also the time of year when many swans are reported dead.

There is some very slight evidence that survival of swans after their sixth year of life is lower than that at earlier ages. However, the evidence is not sufficient to prove this.

It was stressed earlier that the survival figures we have calculated must be regarded as minimal. It is also possible to calculate survival-rates from the ringing recoveries, but apart from practical difficulties the data are at present too few to provide us with accurate answers. However, it is possible to obtain one other estimate of survival, that from the birds that are known to have bred. These are birds that had established themselves on breeding sites and are very unlikely to have moved far in later years. Hence it is highly probable that when such birds have disappeared they have in fact died. Table V gives our data for the survival of these birds. Once again we have not the precise data that we should like in that not every site was visited every year. In the few cases where a site has not been visited for two years and a breeding bird has disappeared it has been assumed that it died in the first of the two years. Hence there will be a slight bias reducing the true survival figure. For this reason little emphasis can be placed on the differences between survival rates in different years. In particular, this error is, in part, likely to have caused the large difference between 1962 and 1963 since coverage was poorest in 1963. However, these errors are unlikely to seriously affect the average survival figures. There do not seem to be marked differences between the survival rates of birds breeding in urban and rural areas (though Reynolds found some variation in chick survival with habitat) nor do there seem to be differences between the sexes; the survival rate for males has been 17.8% and that for females 18.6%.

Table V. Survival of breeding Mute Swans in the Oxford study area.

Year breeding	*No. not known to have survived to next season*	*No. known to have survived to next season*	*% Mortality*
1960	1	6	21.4
1961	5	16	
1962	8	25	24.2
1963	4	48	7.7
1964	19	81	19.0
1965	21	86	19.6
total	58	262	18.1

Life-table and population changes

Clearly the data presented above are not as accurate as we would like, nor based on as many years as would be desirable. However, it is of interest to see whether our figures can be used to provide a life-table for the Mute Swan in which production balances the loss of breeding adults. If we assume that breeding first occurs at four (on average) then we can calculate the number of young per pair which survive to age four (from Table IV above). We estimate that about two young were raised per pair to September and so:—

Each pair hatches 4.0 young.

Each pair raises 2.0 young to September: survival 50% from hatching.

Each pair raises 1.3 young to 1 year old: survival 67% for rest of year.

Each pair raises 0.89 young to 2 years old: survival 67% during second year.

Each pair raises 0.67 young to 3 years old: survival 75% during third year.

Each pair raises 0.43 young to 4 years old: survival 75% during fourth year.

From this it seems as if some 0.4 young per pair per year survive to breed. The figures for adult mortality suggest that about 0.36 birds die per pair per year (Mortality is (1.00—0.82) × 2 for each pair), which is roughly the same as the production to four years.

The data are not nearly sufficient to say whether the production is too many or too few to maintain a stable population. However, data collected by the Wildfowl Trust (Ogilvie 1967) show that there is some fluctuation in numbers of Mute Swans and that they may have been declining in the early 1960s. We have not, however, found much variation in the numbers of breeding pairs in our area, but, if one can assume that a site which is occupied in one year by a pair of swans is a suitable nesting site, then we have more suitable nesting sites than we have pairs of swans. For example in 1966, 148 sites where swans are known to have bred in our area (and which were still considered suitable) were visited, but only 112 of them were occupied by territorial pairs (including non-breeders). We would stress that 1966 was not abnormal in this respect; there have been a number of empty sites in all years since the mid-1950s when censuses started. It would therefore seem that the local population of swans is not at present limited by the number of nesting sites.

Acknowledgements

We are grateful to many people who have helped us with this study. The Wildfowl Trust has supplied us with the numbered rings used in the study. The R.S.P.C.A. officers for this area, Chief Inspectors Ambrose and Hallam have provided us with many reports of marked swans. Many members of the Oxford Ornithological Society have provided us with records of marked birds and nests. In particular, Messrs. R. S. Bailey, M. J. H. Cook and P. J. Wilkinson have helped in the ringing and recording.

Dr. D. Lack kindly read and criticised the manuscript.

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