Pairing and breeding of Mute Swans

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Introduction

The Mute Swan is a species about which numerous legends abound, particularly regarding their faithfulness to their mates and their long life span. When improved swan rings were made available in 1960 the species became an obvious one to study and to test some of these popularly-held beliefs, because of the feasibility of marking and regularly recapturing a large proportion of the population. It was also an opportune time to carry out a study as there were widespread suggestions in the press and elsewhere that the Mute Swan was becoming too numerous and that control measures ought to be taken. Fact finding studies are a desirable preliminary to any control, both in enabling the most effective means to be prescribed and also in preventing or delaying the implementation of actions based on over-hasty decisions. Very little previous work had been carried out on the Mute Swan in Britain, it having been considered too uninteresting a species to ring.

Accordingly the present spare time study was started when the author went to live in south Staffordshire in October, 1960. The principal objects of the study were to examine in detail (a) pairing and breeding; (b) non-breeding herds; (c) moulting; (d) the complete life cycle. The study is still in progress and will continue for several years yet. However, sufficient data have now been accumulated on pairing and breeding for firm conclusions to be drawn on many aspects of the Mute Swan's behaviour. This paper is based on work carried out in the years 1961-67.

Study area

The study area was roughly centred on the author's home at Shenstone, near Lichfield, Staffordshire, and was a rectangle extending 40 km. to the north and 36 km. to the east of National Grid co-ordinate SO.900900 (an area of 550 square miles). This was the maximum size of area which could be covered effectively while containing sufficient Mute Swans (approximately 100 pairs plus 300 birds in non-breeding herds at the start of the study) for the results to be significant. The majority of the area is in Staffordshire, but small parts of N. Warwickshire, N.E. Worcestershire and S.W. Derbyshire are also included. A large part of the area is open farmland traversed by the valleys of the Rivers Trent, Tame, Sow and Penk—the first two being heavily polluted by industrial waste from the west Midlands. These rivers are fed by several fresher and cleaner streams, notably the Mease and the Blyth, which in fact form a more suitable habitat for nesting swans. Canals are also extensive but are not an important habitat for Mute Swans because of pollution, lack of food

and disturbance. However, the most widespread habitat for Mute Swans in the study area is the large number of small pools, typically half to two acres in size, most of which are fringed with reedmace. Some of these pools have resulted from coal mining subsidence in the Cannock and Tamworth areas while many others are 'industrial flashes' in and around the south-western portion of the area, which takes in much of the heavily industrialised 'Black Country.' Gravel pits in the Tame and Trent valleys provide another useful habitat while there are a number of larger lakes of 5-15 acres scattered over the whole area—mainly in the grounds of large estates. The largest individual pieces of water are the Blithfield (800 acres), Cannock and Gailey reservoirs and the most concentrated area of suitable habitat is formed by the numerous subsidence pools of the Alvecote Pools Nature Reserve near Tamworth.

Several small towns—Burton-on-Trent, Tamworth, Stafford, Rugeley, Lichfield and Cannock—are scattered around the more rural parts of the study area and most of these act as centres for non-breeding herds on the rivers running through the towns or on nearby large areas of water. It is fortunate, though largely fortuitous, that there are no other non-breeding herds particularly close to the study area. This has meant that most of these relatively sedentary birds have stood a good chance of being ringed in the non-breeding herds before pairing for the first time. The nearest points to the study area where other non-breeding herds occur are at Leicester (23 miles E.), Nottingham (22 miles N.E.), Derby (8 miles N.E.), Stoke (10 miles N.), Shrewsbury (24 miles W.), Worcester (25 miles S.W.) and Stratford-on-Avon (20 miles S) —but only the last mentioned herd has been ringed (by J. A. Hardman) as extensively as those inside the study area.

Catching and marking

Most of the swans in the study area are rather wild and comparatively few could be enticed close enough with bread to be picked up by hand as they have been on the Thames and elsewhere in England. Most birds were therefore caught with a 'swan pole'—an aluminium shepherd's-crook attached to the end of a 12-14 ft. bamboo pole. Nesting birds were the easiest to catch because their aggressiveness tended to overcome their fear of man (and his swan pole). In particular if the female could be caught first the male would normally attack sufficiently strongly to enable him to be hooked also. Pairs which were not nesting (and the non-breeding herds) were caught after being gently herded, often with boats, into a confined space where they could be reached if they attempted to fly off. A team of ten people, or even twenty for the big flock round-ups, was needed for these operations. No permanent disturbance was caused to the birds by the ringing operations and no desertions of nesting birds resulted.

Most of the work on paired birds took place in March, April and May, when virtually every weekend was devoted to locating, catching and determining the breeding success of this section of the swan population. Family parties were located again in August and September to determine the number of young reared to fledging and to ring them. Regular round-ups of the non-breeding herds took place at various times of the year, including spring, to establish which birds were definitely not paired, and in late July to determine their moulting grounds.

Each spring a high proportion of the paired population of Mute Swans in the study area was caught (Table I).

Swans were ringed on the left leg with a conventional numbered metal B.T.O. ring. Spiral plastic colour rings were added to the right leg to indicate the age of the bird (if known) and the non-breeding herd(s) in which it was found. In addition a yellow plastic ring was added to the right leg of all paired birds and in 1966 to the left leg as well. In 1967 two yellow rings were used on the left leg.

Table I. Number of paired Mute Swans caught in each breeding season.

Year	*Pairs present*	*Both birds caught*	*One bird caught*	*% caught*
1961	92	71	13	*84*
1962	96	83	9	*91*
1963	88	79	5	*93*
1964	98	93	4	*97*
1965	110	99	8	*94*
1966	95	88	5	*95*
1967	81	72	5	*92*

No attempt was made to give birds individual colour codes, this being impracticable with the numbers handled over the period of study. However, a number of birds did collect unique colour combinations as a result of their travels from flock to flock. The use of colour rings in this way enabled limited data to be obtained (e.g. the age) from a bird which could not be caught, and also enabled interesting birds to be recognised and caught for checking of the ring number (e.g. a paired bird which had moved into a non-breeding herd).

The actual colour code (right leg) used was: hatched 1961 (white), 1962 (mauve), 1963 (two white), 1964 (light green), 1965 (black), 1966 (dark green), 1967 (brown); Burton-on-Trent flock (orange), Tamworth/Alvecote (light blue), Cannock Reservoir (dark blue), Stafford (red), Blithfield Reservoir (pink); paired (yellow), paired 1966 (yellow each leg), paired 1967 (yellow right/two yellow left).

The paired population

The number of pairs located each spring remained relatively constant during the seven years, averaging 94 and ranging from a low of 81 in 1967 to a high of 110 in 1965 (Table I). In the first two years up to ten pairs may have been missed, thereafter it is unlikely that more than two or three pairs a year were overlooked. The lower population in 1963 was the result of mortality in the severe winter (Ogilvie 1967). The high population in 1965 and the apparent subsequent decline in 1966 and 1967 is however less easily explained and is considered later in this paper.

Frequent visits were paid to each pair of swans throughout the spring—whether or not they had already been caught—in order to determine their nesting success. It became apparent in the first year of the study that a substantial number of pairs were not going to lay eggs. The percentage of the *paired* population which was non-breeding (Table II) was remarkably constant from year to year at about 30%. The high percentage (37%) of non-breeding pairs in 1963 reflects the preceding cold winter, which killed off many of the regular breeding birds, and the subsequent late spring which prevented others from coming into breeding condition in time to nest.

The low percentage (23%) of non-breeding pairs in 1967 was due to a low recruitment of young birds from the non-breeding flocks which had suffered an overall decrease, and to the oiling disaster at Burton-on-Trent in 1966 (see later). There were only two non-breeding pairs within a 10 km. radius of Burton in 1967 compared with eight in 1966 and six in 1965. The number of breeding pairs, which were unaffected by the oil, was similar in all three years.

The existence of non-breeding pairs had been noted before at the time of the 1955-56 and 1961 national censuses (Campbell 1960, Eltringham 1963) but in only a few areas was the non-breeding portion of the paired population as high as in the present study. However, this could be due to non-breeding pairs being overlooked rather than to a major variation from one area to another. Evidence to support this suggestion comes from the 1955 census in the Staffordshire study area which recorded only 6% of the pairs as non-breeding.

The behaviour of non-breeding pairs varies considerably from one pair to another. Some are very similar to breeding pairs in that they hold a defined territory on a stretch of water throughout the spring, driving off all intruding swans, and displaying regularly to each other. Many even build part nests. A few remain together on their territory throughout the year but most return to the non-breeding herds in June, prior to moulting. Other non-breeding pairs are much more loosely associated, often holding territories on one vacant water after another, sometimes two or three miles apart, and frequently only remaining paired for a part of the

Table II. Division of paired population between breeding and non-breeding pairs of Mute Swans.

Year	*Total pairs*	*Breeding pairs*	*Non-breeding pairs*	
			No.	*%*
1961	92	69	23	*25*
1962	96	66	30	*31*
1963	88	55	33	*37*
1964	98	72	26	*27*
1965	110	78	32	*29*
1966	95	68	27	*28*
1967	81	62	19	*23*

spring (as little as 3-4 weeks) before adjourning again to the non-breeding herds. Non-breeding pairs are not normally aggressive towards human intruders in the same way that nesting birds are and a non-breeding male will rarely attack even if its mate has been caught.

Most pairing originally takes place in the flocks. Pairs may even be observed displaying to each other within the non-breeding herds in the spring but only those pairs which have actually split away from the flock completely have been considered in this study. The roving and transient nature of many non-breeding pairs may account for many not being recorded in censuses based on one visit to each water or on an aerial survey. Thus the 20% of pairs holding territories, but without nests, recorded by Eltringham's 1961 aerial surveys is probably a mixture of failed breeders and non-breeding pairs still remaining together at the time of the census.

The density of pairs in the study area was approximately one pair for every 5½ sq. miles. Other published data refers mainly to the density of breeding pairs and in the Staffordshire study area the number of breeding pairs average 70 each year (omitting the exceptionally low figure of 55 pairs in 1963) giving a density of one breeding pair per 8 sq. miles. The 1955 census (Campbell 1960) gave an estimated average density of breeding pairs in England and Wales of approximately one pair per 16 sq. miles (estimated 3,500 nesting pairs in 58,000 sq. miles). Only in Middlesex (one per 3 sq. miles) and Dorset (one per 7 sq. miles) was a higher density than for the present study actually recorded. In Staffordshire as a whole the breeding pair density was recorded as one pair per 12 sq. miles and Campbell's estimate that about 25% of the nesting pairs were missed therefore seems to be near the truth as far as Staffordshire is concerned if allowance is made for the 'swanless' areas of the north Staffordshire moors.

Examination of the 1955 records for the present study area shows that 64 nesting pairs were recorded. These were mainly situated in or near the heavily populated areas or at waters regularly visited by bird watchers. There is a conspicuous absence of records from the remoter pools and areas of streams and rivers known to be used regularly by nesting pairs throughout the period 1961-66. Since these particular habitats have remained largely unchanged since 1955 it is likely that most of these were in fact occupied then. It is estimated therefore that the true breeding population of the study area in 1955 was around 85 pairs. This had declined to about 75 pairs in 1961, contrary to the national trend which indicated similar numbers of breeding pairs in both years. However, much of this decrease had probably taken place in the Black Country due to the disappearance of habitat by the filling in of industrial flashes and the draining or cleaning out of canals. In this part of the study area 15 nesting pairs were recorded in 1955 (probably an accurate figure for it is an area heavily populated by humans), compared with five in 1961 and only three in 1966. The total paired population in this region had dropped from 16 pairs in 1955 to 8 pairs in 1961 and 1966—the increase in the proportion of non-breeders being a further indication of the present unsuitability of the area for nesting.

During the period 1961 to 1967 there has been a marked decrease in the population of the non-breeding flocks in the study area—from approximately 330 birds in April 1961, to around 140 birds in April 1966. The 33% decline from 1961 to 1966 is similar to that noted from much of the remainder of England and Wales over the same period (Ogilvie 1967). This makes the comparative constancy of the paired population—both breeding and non-breeding—all the more remarkable.

The sharp decrease in numbers in the non-breeding flocks between 1966 and 1967 was due to the oiling of the whole of the summer moulting population at Burton-on-Trent (the largest flock in the study area) which resulted in the death of between 80 and 90 birds.

The percentage of the population which is paired each spring has increased from around 40% in 1961 to nearer 57% in 1966, while the percentage of the population actually nesting has increased correspondingly from just under 30% to nearly 39%. The figure of 30% for 1961 agrees very closely with the figures given by Campbell and Eltringham for the 1955 and 1961 censuses; they found approximately twice as many non-breeding birds as breeding birds. The figure for the study area is probably a little lower than it really should be because its arbitrary boundaries contain rather more than its fair proportion of non-breeding flocks.

Age

The age of Mute Swans can only be determined with certainty until about August following the year of hatching and therefore there was no direct way of telling the age of the paired birds present at the start of the study. However, as the

study has progressed an increasing proportion of the paired population has been of known age, having originally been ringed as pulli or as first-year birds. Thus it has been possible gradually to build up information on the ages at which Mute Swans pair and breed for the first time, and on the age structure of the breeding and non-breeding paired populations.

As such a high proportion of the paired population is caught each spring and as the non-breeding flocks are rounded up at this time of the year also, it has been possible to determine with fair certainty when birds have *paired* for the first time. Altogether 125 of these have been of known age (Table III). Nearly half were two years old and a further 30% were three years old; most swans can therefore be said to pair for the first time before they are four years old. A few even take mates when only one year old, while still in their brown-flecked immature plumage. (One year old birds are also frequently seen displaying in the spring within the non-breeding herds.) On the other hand, some birds do not take mates until they are five or six years old. Others have remained in the flocks for this period without ever pairing. This aspect will be covered in more detail in a subsequent paper dealing specifically with the non-breeding flocks.

The majority of birds have at least one non-breeding year paired before they commence nesting. Age plays an important part in the proportion (nearly a quarter) of birds which paired and bred for the first time in the same year. Only two out of 60 birds pairing first at one or two years old nested in the same year, compared with over half those paired for the first time at age four and over.

There are no major differences in these patterns between male and female birds. However, there is a slight tendency for female birds to be more precocious; four out of the five pairing at one year old and both birds which nested at the age of two were females. Males and females pairing for the first time at the age of three seem equally likely to breed in the same year.

The age of *breeding* for the first time is known for 60 Mute Swans (Table IV). Half nested and laid eggs for the first time at the age of three and a further third at the age of four—a pattern similar to that of first pairing but one year later. Most swans can therefore be said to commence nesting at the age of three or four. At these ages there was no difference between the sexes but only females have been known to nest at the age of two, whilst most of the birds not nesting for the first time until the age of five were males. This appears to confirm a slight tendency for females to mature earlier than males. These figures are very similar to those given by Perrins and Reynolds (1967) from their study of Mute Swans breeding around Oxford.

Birds ringed after their first year cannot be assigned to a definite age group, but only to *minimum age*. Ages of birds in 1961 and 1962 are omitted from Table IV as they would have incorrectly inflated the minimum age 2 and 3 years categories. The minimum ages still throw some light on the period which may elapse before nesting for the first time. It can be seen that a substantial percentage (12%) of swans live for five or more years before breeding. Four birds did not breed for the first time until at least six years old. There is again a tendency apparent for such old birds to be male

Table III. Age of Mute Swans at first pairing.

	Age and sex												
	1		2		3		4		5		6		*Total*
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Breeders	—	—	—	2	9	7	6	5	3	1	—	1	34
Non-breeders	1	4	24	29	10	12	4	5	1	1	—	—	91
All paired birds	5		55		38		20		6		1		125

Table IV. Ages at which Mute Swans bred for the first time.

	2 years		*3 years*		*4 years*		*5 years*		*6 years*		*Total*
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Actual age	—	2	14	12	11	10	7	2	1	1	60
Minimum age	17	29	21	20	19	9	8	3	2	2	130

and for more of the youngest age group to be female.

Although no one year old birds have been recorded nesting, two birds one and a half years old have been found with a mate and a brood of juveniles. The first was a male bird caught in early November paired to an unringed female, which continued to breed in the same area in subsequent years with a new mate. The male had not been seen since the previous December, when it was ringed as a first winter bird in a flock outside the study area, so nothing is known about its whereabouts during the intervening breeding season. The other bird under two years old with a family was found in early January and had been ringed as a one year old bird in a moulting herd the previous July. Its mate was not caught and its sex not determined. Although both parties of two adults and two juveniles were behaving exactly as a normal swan family, it seems most unlikely that either of the one and a half year old birds had been a parent of the young, since breeding even at the age of two is very rare. It is more likely that these young birds paired up with the adult of the family during the autumn, possibly replacing a mate which had died since the breeding season.

Age structure of the paired population

An accurate assessment of the age structure of the breeding paired population will be possible as more of the birds of unknown age drop out. An indication is however afforded by the situation in 1966 (Table V) when it was known that 70% of the birds were at least five years old, 50% at least six. In 1967 almost 60% were at least six years old and 37% were seven, but this may not be a typical age structure. Two females were then at least eleven and one male at least nine years old. At the other end of the scale, at most 15% of the population was under four years old in 1966.

In the case of 59 non-breeding pairs the situation in 1965 and in 1966 indicated that 25% of the birds were at least five years old, 16% at least six, and, conversly, that 61% were under four years.

Table V shows that there is a tendency for males and females in a breeding pair to be of similar age. But detailed examination of the data for 1963 to 1967 shows there is more likelihood of the male being older than the female, in 116 breeding and 58 non-breeding pairs, rather than *vice versa*, in 88 and 45 pairs. This again suggests an earlier maturing of the female.

There is a strong tendency for birds taking a mate for the first time in their

Table V. Age structure of breeding pairs of Mute Swans in 1966.

Age of female	*Age of male* 2+	3	3+	4	4+	5	5+	6	6+	7+	8+	All
2+	1											1
3	1	1			1							11
3+			1		1	1	2		3			
4			1	1								9
4+				1	3	1	1		1			
5			1	1	1				4	1		20
5+				1		2	1	1	3	3	1	
6			1					2				14
6+					1		1		7	1	1	
7+			1						4	6		11
8+												—
9+												—
10+								1	1			2
All	2		6		11		9		27	11	2	68

life to select a bird of similar status. For instance, in the years 1963-67 out of a total of 292 birds recorded as paired for the first time 218 (74%) were paired to birds which were also never known to have been paired before. This might be expected since much of the pair selection takes place within the non-breeding herds. These flocks are largely composed of birds which have not paired before, especially after those pairs which have come into the herd for the winter have departed in late January and early February to resume their territories. Birds paired for the first time with a previously paired bird are in most cases replacing lost (dead) mates.

Of all the swans thought to be paired for the first time 121 (41%) went on to nest in the same season. This is higher than the figure of 25% for birds of *known* age breeding in the first year, the difference probably being due to more older birds being of unknown age and to those pairs which had been missed in the earlier years of the study. Being mated to a bird which had previously been paired did not appear to have much effect on the chances of a newly paired bird settling down to nest. Thus the pairs which went on to breed included 35 (29%) with one experienced bird, while those 171 pairs that did not breed included 33 (23%). It is concluded therefore that sexual maturity, which is linked mainly with age, is the main criterion for determining whether a bird will breed on the first occasion it is paired.

The percentage of the total paired population which was composed of birds paired for the first time varied markedly from year to year in the period 1963-67 (Table VI). The high figure of 46% in 1963 was largely due to the high mortality during the severe weather in January and February 1963 leaving many vacancies in the paired population to be filled by new birds. The figures for 1964 and 1965, when around a third of the total paired population was paired for the first time, are probably a truer reflection of the normal figure. In 1966 and 1967 only 20% of the paired population was paired for the first time and this low figure seems to be mainly associated with an unusually low number of first time paired breeding birds.

The percentage of the breeding population composed of first time paired birds has fallen partly due to the increasing percentage of the existing breeding population which has survived (see later), itself due to the series of mild winters which have followed the severe winter of 1962-63. It could, in addition, be due to the comparative lack of birds three or more years old (the ages at which breeding in the first year paired is most likely to occur) in the non-breeding herds, due to the low number of young reared to fledging in 1963 (see later) and the heavy mortality in the 1962-63 winter of young reared in 1962 or before. However, a lack of such birds was not apparent in the 1965 non-breeding paired population as would have been expected if this explanation was correct.

The percentage of the non-breeding paired population which is paired for the first time has been relatively constant in the period 1963-67, and the level indicates clearly that a high proportion of non-breeding pairs contain at least one bird paired for the first time. Nevertheless the actual number of individuals involved in 1967 was significantly lower than in any previous year, again indicating a paucity of new blood available.

When birds paired at least a year previously and now breeding for the first time are added to those pairing and breeding for the first time in the same year, the overall percentage of new breeders in the paired population was 43%, 44%, 26%, 11% and 20% in 1963-67.

In the period 1963 to 1966, non-breeding pairs, for which the age or minimum age of both birds are known, included only 25 cases where *both* birds were aged four or more. This suggests that immaturity of one or both members of a pair is the main reason for non-breeding. In these

Table VI. Mute Swans paired for the first time showing the proportions they represent of the paired population.

	Breeding		*Non-breeding*		*All birds*	
	No.	%	No.	%	No.	%
1963	38	*35*	43	*65*	81	*46*
1964	34	*24*	32	*62*	66	*34*
1965	25	*16*	48	*75*	73	*33*
1966	8	*6*	30	*56*	38	*20*
1967	16	*16*	22	*58*	38	*24*

older pairs unsuitability of habitat—lack of food, no nesting site, human disturbance—is considered to have been the limiting factor in ten cases. Sometimes, despite deterioration of habitat since the previous breeding season, such as infilling of pools by tipping, the resident pair clung to the territory. The remaining 18 cases may have included birds maturing unusually late or newly-paired birds not settling down in time to nest. In one case the female was almost certainly infertile. But there remain six cases in which a pair that had previously bred together which did not breed in a subsequent year in spite of remaining together on an apparently unchanged territory and habitat. Three of these pairs subsequently resumed breeding together in the following year and another pair after a gap of two years. It is probable, therefore, that one or both of the birds in these six pairs did not come into breeding condition for some reason in the seasons in which breeding was missed.

One pair, of unknown age but said to have been present at the same park site for many years, reared young for the first time in 1961 after having their eggs stolen in all the previous years. They seemed so 'overjoyed' at having a family to rear that they made no attempt to drive off their young and no attempt to breed in 1962. The two young eventually stayed with their parents until the 1962 moulting period. Another pair kept their young of 1966 until the summer of 1967 and did not nest, though in this case they had reared young in the previous year. At another site two of a brood of five young reared in 1966 remained with their parents until at least the end of May 1967, but in this instance the adults were not inhibited from nesting at the same time. The same pair is usually the last to drive off its young from the previous year and in 1964, after rearing young for the first time in 1963 after failures in 1961 and 1962, this did result in egg laying taking place much later than in other established pairs.

Non-breeding pairs remaining together but not breeding for two consecutive years have been recorded on seven occasions when at least one of the pair has not been known to be more than three years old. Sexually immature three year old birds were probably the cause of non-breeding in four cases, unsuitable territories in two cases and infertility of what was probably an old female in the remaining case. Only one pair eventually survived together to a third season and this pair then bred successfully.

Mortality

The mortality rate of the paired population in the study area can be calculated each year from knowledge of the number of birds known to survive from one breeding season to the next. This method is possible because of the high percentage of the paired population which is caught each spring and the relatively sedentary nature of the species, particularly once paired. Since the non-breeding herds are regularly rounded up, those birds which are still alive but not paired in the subsequent season can also be detected.

The survival of paired birds from one year to the next (taken from 1st April to 31st March to coincide with the breeding year) is given in Table VII separately for breeding and non-breeding birds since there are significant differences in the age

Table VII. Mortality rate of paired Mute Swans.

Season (1st April to 31st March)	*Alive on 1st April of first year*	*Still alive on 31st March of next year*	*Dead by next 31st March*	*Missing after next 31st March*	*Minimum mortality rate*	*Maximum mortality rate*
Breeding birds					%	%
1961/62	122	100	4	18	*3*	*18*
1962/63	127	86	14	27	*11*	*32*
1963/64	107	79	10	18	*9*	*26*
1964/65	141	113	6	22	*4*	*20*
1965/66	153	129	5	19	*3*	*16*
1966/67	136	101	12	23	*9*	*26*
Non-breeding paired birds						
1961/62	33	17	5	11	*15*	*48*
1962/63	48	31	9	8	*19*	*35*
1963/64	56	39	6	11	*11*	*30*
1964/65	49	33	5	11	*10*	*33*
1965/66	54	29	11	14	*20*	*46*
1966/67	45	22	5	18	*11*	*51*

structure and habits of these two sections of the paired population which could lead to different mortality rates. The minimum mortality rate for each year is determined from the number of birds definitely known to have died, while the maximum mortality rate is determined by adding to this all birds never subsequently seen after 31st March of the year following. In practice some of these latter birds may have emigrated from the study area and may still be alive, while a few may have been living, uncaught, within the study area. However, the true mortality rate is probably close to the maximum rate.

For the paired breeding birds the usual maximum mortality rate would appear to be around 20%. Perrins and Reynolds (1967) give 18% for their breeding birds around Oxford. It was highest in 1962-63 due to the exceptionally severe weather that winter. The maximum mortality rate of paired non-breeding birds has a usual level around 35%. The high rate in 1961-62 might indicate that this segment of the population suffered more severely from the cold spell that winter than did the breeders. However, too much reliance should not be placed on figures in this first year of the study. The maximum and minimum rates in the non-breeders show a much lesser degree of association than they do in the breeders. It may be that the maximum rate for non-breeders is less reliable and more prone to influence by birds moving out of the area owing to a lesser attachment to a particular territory.

The combined data for breeding and non-breeding pairs in Table VII gave maximum mortality rates of 24%, 33%, 28%, 23%, 24% and 32% in the six seasons. The true mortality of the paired segment of the population is thus around 25%. This is of course remarkably high for a bird as large as a Mute Swan which has so few natural enemies. Ogilvie (1967), considering the complete swan population over one year of age, deduced a mortality rate of 38%. However, his data are based largely on recoveries of birds ringed in non-breeding flocks most of which are not more than three years old. Although experience may help older Mute Swans to avoid flying into objects (the major cause of death) another reason for the different mortality rates is probably the *amount* of flying done by the different sections of the population. Breeding paired birds fly comparatively little in the months March to September. Non-breeding paired birds, on the other hand, tend to move around more in the breeding season and then often join the non-breeding flocks from June onwards. Birds from the non-breeding herds fly around a lot at all times of the year, except in the July-August moulting season. Thus although younger less experienced swans are likely to have rather more fatal accidents per mile flown, a further cause of the differential mortality rates in different section of the population is the relative number of miles flown per year by the different groups.

Although Mute Swans are probably able, potentially, to live to a considerable age, their chances of surviving for many years the hazards of the obstacles set around the countryside by man are small. Only those pairs with territories in relatively artificial surroundings where flying is rarely possible are likely to achieve their full life span.

It seems as if the wheel has now gone full circle. After causing a major increase in the swan population by providing food to sustain large non-breeding flocks in areas where little natural food exists (particularly in the winter), man has now tipped the scales the other way by placing an ever increasing number of obstacles such as electricity wires (so frequently sited in river valleys) in the way of flying birds.

In Table VIII the breeding pairs are sub-divided on the score whether they were successful or unsuccessful in rearing

Table VIII. Mortality rate of successful and unsuccessful breeding Mute Swans.

	Successful breeders			*Unsuccessful breeders*		
Season	*Alive on 1st April of first year*	*Dead or missing by 31st March next year*	*Maximum mortality rate (%)*	*Alive on 1st April of first year*	*Dead or missing by 31st March next year*	*Maximum mortality rate (%)*
1961/62	48	7	*15*	49	12	*25*
1962/63	76	24	*32*	50	17	*34*
1963/64	64	11	*17*	43	17	*40*
1964/65	84	12	*14*	57	16	*28*
1965/66	97	17	*18*	56	7	*13*
1966/67	68	10	*15*	68	25	*37*

young during the years in question. In four of the years the successful breeders have a markedly lower maximum mortality rate than the unsuccessful breeders. Their advantage appears to be absent when the winters are exceptionally severe (1962-63) or mild (1965-66). The generally different levels may be related to a difference in the amount of flying normally done by the two groups. Failed breeders tend to behave more like non-breeding paired birds, joining the herds and moving around from place to place.

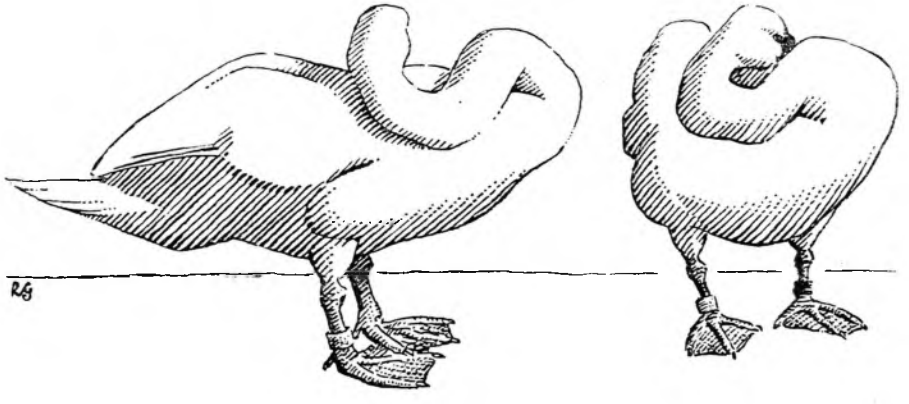
A useful piece of information deriving from this method of assessing mortality rates is an indication of the percentage of dead birds that is found and reported. Of 296 paired birds which disappeared from the study area 92 were reported dead, close on one-third. In areas less intensively combed by ringers or less densely populated by man the proportion is probably rather less.

The stability of pair bonds

If we wish to consider the strength of the pair bond, the tendency of birds to remain paired from one year to the next, we must obviously eliminate from consideration birds which were dead or missing by the following year. This is the more so as we have already seen (Table VII) that there is a difference in mortality according to whether paired birds are breeding or non-breeding. In Table IX the marital status of paired swans in the following year is set out. Of the birds that were paired and breeding in one year and alive in the next, about 85% were still paired together. The severe winter of 1962-63 obviously had a disruptive effect on the pairings of survivors, only half of the 1962 birds remaining paired together in 1963. Furthermore, a fifth of the survivors had not found new mates, probably because they lacked the time or were in no condition to take a new mate that season.

Table IX. Marital status of Mute Swans in following years.

Year	*Alive*	*Status in following year*				
		Dead or missing	*Same mate*		*New mate*	*Not paired*
			No.	%	%	%
Breeding						
1961	100	22	84	*84*	*5*	*11*
1962	86	41	46	*54*	*24*	*22*
1963	79	28	68	*86*	*6*	*8*
1964	113	28	98	*87*	*7*	*6*
1965	129	24	108	*84*	*12*	*4*
1966	101	35	88	*87*	*11*	*2*
Non-breeding						
1961	17	16	14	*82*	*6*	*12*
1962	31	17	10	*34*	*33*	*33*
1963	39	17	18	*46*	*37*	*17*
1964	33	16	26	*79*	*6*	*15*
1965	29	25	12	*41*	*31*	*28*
1966	22	23	12	*55*	*32*	*13*



The stability of the pair-bond of non-breeding paired birds was likewise adversely affected by the cold weather of 1962-63. The high figure in 1961 was probably spurious, associated with the first year of the study, but that in 1964 was genuine, though unexplained, and contributed to the unusually high paired population in 1965. It would certainly seem that the pair bond is more likely to be disrupted before breeding has taken place. However, several pairs in which both birds were young and paired for the first time have been known to spend one spring together without breeding, subsequently adjourned to the flocks and then re-paired the following spring. It seems therefore that they were able to retain the ability and desire to take the same mate again even though the pair bond appeared severed.

No significant difference in pair bond strength is shown between successful and unsuccessful breeders. Of birds surviving to the following years 82% of the former and 78% of the latter remained paired together.

The combined effect of mortality and divorce results in a continual fall in the number of pairs which remain intact over a period of years (Table X). There is no indication that the year to year survival rate changes the longer a pair remains together. Out of 71 pairs in which both birds were known in 1961, only three (4%) were intact in 1967. The magnitude of this decrease is in part due to the occurrence of an exceptionally severe winter during this period but even without this only 16% of pairs would have remained intact.

Those swans which survive as paired birds for several years are likely to have a number of different mates during their lifetime. During the seven years of the study, 22 birds, 14 males and 8 females have been known to have had at least three different mates. Three birds have even had four different mates. Nine birds had different mates in three consecutive years.

An example of how varied the breeding career of a swan can be is shown by the following example of a male bird:

1961	mate A, nested, success not known.
1962	mate A, nested, reared four young.
1963	alone on territory.
1964	mate B, did not nest.
1965	mate C, did not nest.
1966	mate D, did not nest.
1967 (March)	alone on territory.
1967 (May)	found dead.

The bird was on the same territory each year except in 1964, when it was on another stretch of canal two miles away and its original territory was occupied by another pair.

It has already been noted (Table IX) that some birds paired and breeding in one year have been alive in the following year but not known to be paired. Of 34 such males, 14 were found alone on the territory, but only 2 out of 16 such females. In the case of non-breeding pairs only 3 out of 18 males and none of 17 females were on the territory. Thus breeding males alone seem to have a strong tendency to remain in the original territory. The others probably return to the herds, where, in fact, 2, 3, 4 and 7 of the four categories were recaptured. Breeding males are thus less likely to meet up with an unpaired female and the chances of re-mating are further reduced by the aggressive reaction of even an unpaired male swan to intruders on its territory. One male swan, of a pair which had bred together for five years (the last four successfully), showed a remarkable attachment to its nesting territory. After its mate was shot in early March 1967 it built a complete nest on the usual site and incubated the empty structure for six weeks, a sad sight. However, in spite of the fact that many bereaved swans do return to an environment where they should be able to find a replacement mate quite easily, some seem to remain in the herds without re-pairing for one

Table X. Survival of pairs in the Mute Swan over a period of years.

		Pairs remaining intact until:											
		1962		*1963*		*1964*		*1965*		*1966*		*1967*	
Year	*Known pairings*	*No. of pairs*	*% intact*	*No. of pairs*	*% intact*	*No. of pairs*	*% intact*	*No. of pairs*	*% intact*	*No. of pairs*	*% intact*	*No. of pairs*	*% intact*
1961	71	49	*69*	18	*37*	13	*72*	8	*61*	6	*75*	3	*50*
1962	83	—		28	*34*	22	*79*	12	*55*	10	*83*	6	*60*
1963	79	—		—		43	*54*	31	*72*	22	*71*	13	*59*
1964	93	—		—		—		62	*67*	42	*68*	29	*67*
1965	99	—		—		—		—		60	*61*	37	*62*
1966	88	—		—		—		—		—		50	*57*

or more years. Thus there is some evidence to support the legend that a swan losing its mate will not take another.

Many individuals which fail to take a mate in the season following one in which they have been paired will eventually pair again in a later year. This is true both of birds which remain alone on their territory and those which move into the herds. However, there is sometimes a gap of two or three years before re-pairing occurs and in a few cases individuals appear to have given up pairing for good. For instance, a male bird which had probably bred for several years on the same territory with the same female divorced its mate after the 1962 season. It remained alone on its territory in 1963, 1964 and 1965 and had still not been known to pair again when it was reported dead in early 1967.

Another swan, a female, took a mate for the first time in 1965 when it was at least six years old. It did not breed and its mate was subsequently killed. It then rejoined the flock and had still not taken a mate again when it was last seen in April, 1967.

Birds which have bred and then taken a new mate show a strong tendency to return to their original territory. This holds for males (19 out of 25 cases) and for females (29 out of 40). Birds which had not bred although paired showed a less strong attachment to their territory when taking new mates. About half were found on new sites (10 of 26 males and 9 of 17 females).

Divorce and change of mates

The usual reason for a change of mate was the death or disappearance of the old mate. Cases of true divorce, when both the original partners are known to be alive, account for some of the changes. Among paired non-breeding birds divorce was noted in 11 out of 44 cases of mate-change (25%), whereas it occurred in only 9 out of 65 cases (14%) of changes in breeding pairs.

These figures refer only to divorces where one or both of the divorced birds took a new mate in the following breeding season. Quite a number of pairs also broke up without either bird taking a new mate, at least in the following year. The total number of true divorces among birds which were paired in the years 1961 to 1966 was 52, i.e. in 26 pairs both birds were alive the following breeding season but were not paired together. Half of these were breeding pairs (representing a divorce rate of 3%) and half were non-breeding pairs (a rate of 9%). Just under a third of both groups had taken a new mate by the following year. The disruptive effect of the severe winter of 1962-63 has probably inflated the divorce rate figures, for 22 of the divorces occurred in that season including 16 of the 26 divorces of breeding birds. In three years only two birds divorced and twelve birds divorced in each of two other years.

Some divorce histories are quite complicated, as when mates are exchanged between pairs on adjacent territories. In one case the respective pairs occupied adjacent territories on a group of small rushy pools and an adjoining stretch of canal. Territorial fighting regularly took place and it was presumably in one of these battles that the exchange of mates took place. The males occupied the same territories each year and it was the females which changed in 1963 and changed back again in 1964. All the birds involved had a history of nest failures or non-breeding and the divorces may have partly accounted for neither pair breeding in 1963 and only one of the pairs in 1964.

The circumstances of the exchange of mates between another two breeding pairs between the 1965 and 1966 breeding seasons could not be more different. Both pairs had successfully bred in 1964 and in 1965. They occupied adjoining stretches of an attractive 20 ft. wide stream. Each had a territory one to two miles long and the nest site was usually about two miles apart. On 20th March 1966, one pair was caught, still together, on its usual territory but there was no sign of a pair on the other territory. Returning to the latter territory on 22nd May 1966, the expected female bird was located on a nest at the usual site but the accompanying male bird was the one from the other territory. On revisiting the territory checked in March the usual female was present on a nest, with the male bird from the other territory in attendance. Thus after two successful breeding seasons together the pairs had both divorced and, surprisingly, it was the male birds which had changed territories. Presumably the interchange took place during a border dispute. Both of the new paired combinations successfully reared young and both pairs remained together in the 1967 season also.

A male bird of a pair which had nested successfully together for at least two years had its mate taken by a new male the following year. It remained alone on its territory and then re-paired again to its original mate after the lapse of a year. 'Come home, all is forgiven' may have been its motto.

The divorce percentages given above rather underestimate the frequency of divorces in Mute Swans as they only refer to divorces from one breeding season to the next. A number of mate changes within the same season have been recorded. For instance, two birds caught paired together (both paired for the first time) on 17th March were both found with new mates on 28th April. The male was on the same territory with a new mate and this pair did not breed. The female was on a nest on a new territory about a mile away. Both of the new birds were also paired for the first time. These new pairings remained intact until both of one pair were killed two years later and one of the other pair was killed after four years.

Another bird which divorced its mate in mid-season was one of a pair originally caught on 11th February. The female was found with a new mate on 8th April but although they remained together all summer they did not breed. This pair then also split up and each bird took a new mate the following year—the female therefore having had two divorces in the space of a season. The original divorced male also took a new mate the following year.

Other mate changes within the same breeding season were not necessarily attributable to divorces. For instance, a female was caught on 13th March still paired to the same mate as the previous year, but was recaptured on 20th May at a different site with a new mate. Since the original mate has not been seen again, it was probably dead. A very rapid replacement occurred one year when a male was killed by flying into wires on 6th April just as it was at the nest building stage with its mate from the preceding year. The bereaved female disappeared almost immediately but had returned by 20th April with a new mate. Although this new pair completed the nest they did not actually breed until the following year. Similarly a male whose mate was shot at the end of March had obtained a new mate by the end of April. Yet they did not breed that season although both were four years old and the female had bred the previous year.

A number of instances of birds, paired in the spring with one mate, being caught with a new mate in the following autumn or winter, have been recorded. In most cases the pairs involved had been non-breeding or failed breeders. For example the male bird of a non-breeding pair had divorced the female and taken a new mate by the following November. Similarly, the female of an unsuccessful breeding pair had a new mate by the following December, having divorced its previous mate. In a third pair, also failed breeders, the fate of the male bird was not known but the female bird was with a new mate by December. All three of these pairs cited remained together and bred in the following season while neither of the birds left without a mate by the divorces took a mate the following year.

Two possible instances of changes during the year in successful breeding pairs, involving new mates less than two years old, were mentioned earlier. In another, definite, case the male of a pair nesting together in April was found with a new mate and a brood of two juveniles at the same place in December. The original female was not seen again and was presumably dead. The new female remained at the same site the following year but with a new male bird—the original one having also disappeared, presumed dead.

The other instance was actually witnessed. The male bird of a pair which had nested together for at least two years was driven off by an unpaired intruding male from its mate and brood of 4 two month old unfledged young. The female took no part in the battle and after it was over sailed off down the stream with the new mate and the rest of the family as if nothing had happened. This female was not seen the following year and was therefore probably dead. Neither male was then paired but the original male had returned to his old territory.

Another unusual incident which was witnessed occurred in September when three adults were found displaying to one another. Two of these were an established pair—the performance took place in the presence of their offspring—and the third was a previously unpaired male bird. It is not clear why such an intrusion on their territory was tolerated by the pair but their bond survived the incident and they remained together in the following season. The other male bird found a mate the following year also.

These autumnal changes of mate suggest that there is then a resurgence of pairing activity in the Mute Swan. Pairs have been observed at this time of the year without the yellow colour rings denoting a previously paired bird. Furthermore, pairs have later been found in which both birds were known to have been present in the same moulting flock the previous summer and it is possible that these paired in the flock and left together in the autumn. The extent and

role of autumn pairing will be studied further in the future.

This section on odd pairings may perhaps be concluded by two examples of the pairing of closely related birds—though neither pair actually bred. In one case a one year old male bird remained with its mother for the whole of its first spring, after its father had died and the rest of the brood had dispersed. Mother and son displayed to each other and held a territory just like a normal pair and the partnership did not dissolve until the July moulting season.

The other instance involved a female bird found paired in October to one of its two-and-a-half year old offspring. They were attempting to drive off the pair of swans which had taken, during the previous spring, the territory which had belonged to the parents of the male in the two preceding years. After losing their territory the original pair had split up; the male remained unpaired and the female was not seen until this occasion in the autumn, so it is possible that it had even been paired to its two year old youngster in the spring also. The female was not seen again after October and the young male took a new mate the following year, eventually carrying on to breed on the territory where it had originally been reared.

Movements

Mute Swans move around a fair amount from flock to flock before they eventually take a mate and hold a territory. These movements will be described in a future paper. This section deals only with movements subsequent to the taking of a territory for the first time—changes of territory—and movements of paired birds outside the breeding season.

Once a Mute Swan has established a territory it tends to return there in subsequent breeding seasons even though it may have been away for several months since the end of the previous breeding season. The affinity is strongest in breeding birds, particularly those which have nested successfully. Only three out of the sixteen birds which changed territories by more than five miles had previously bred, and it may be significant that two of these birds had had their previous mates shot. Most of the birds which moved far had lost (or in two cases divorced) their previous mates and only two complete pairs changed territories by more than five miles. The greatest shift in territory was 17 miles. Only 2% of the total surviving paired population moved its territory more than five miles from the previous year.

One bird changed its territory by more than five miles three times, although one of these related to pairing in the autumn:

May 1961	nested unsuccessfully.
Jan. 1962	13m. NNW, in flock.
Feb. and Mar. 1962	14m. SE, in flock
Sept. 1962	6m. N, pair, new mate.
Jan. 1963	6m. S, in flock.
May 1963	3m. E, paired, new mate, nested successfully.
1964 and 1965	same territory and mate, nested successfully.
1966	not seen again — presumed dead.

Many pairs or individuals have been recorded changing their territory by distances less than five miles. Although in some cases this is the result of territorial fights, in other cases there was no obvious reason. For instance, one pair after nesting for three years at one site (the last time successfully) moved to a new site four miles away (never previously occupied by a pair of swans), leaving their old site vacant. In spite of nesting successfully again they returned to their old site for the following two seasons, both times being unsuccessful.

One female swan has had a remarkably eventful breeding career, occupying three territories and having four mates in six breeding seasons:

April 1961	in flock, 1st winter (i.e., age 1).
May 1962	8m. S, paired, did not nest.
May 1963	same territory and mate, nested unsuccessfully.
April 1964	5m. SW, new territory and mate, nested unsuccessfully.
April 1965	same territory and mate, nested successfully.
May 1966	4m. NE, new territory and mate, nested unsuccessfully.
Feb. 1967	4m. SW, alone on 1964–65 territory.
March 1967	4m. NE, same territory, new mate.
26 Mar. 1967	shot.

The most frequent movement of paired swans is from their territory into one of the non-breeding herds, usually the nearest. Such movements of non-breeding pairs or failed breeders take place extensively in June, prior to moulting in July. This results in up to a third of some moulting herds being birds which paired

in the spring. Successful breeding pairs and others which have stayed on their territory to moult often move into the herds during October to February, especially during hard weather when their territories become frozen over. Although pairs appear to merge completely into the flocks and the pair bond appears to have broken down, they nevertheless usually emerge paired again in late winter. Birds losing a mate travel to a herd and are frequently found back on their territory, paired with a bird from the herd they were known to have visited.

Movements are usually of less than ten miles and only about twenty paired birds, representing about 5% of around 450 individuals known to have been paired in the period 1961-67, moved further than this from their territory. However, some pairs have travelled together up to twenty miles and then returned to their orignal territories. Other individuals have travelled further. A non-breeding paired bird which held a territory in the spring was recovered dead 47 miles away in September of the same year; a failed breeder was reported 28 miles away the following February. There thus appears to be a tendency for non-breeding paired birds or failed breeders to move around over greater distances than successful breeders.

Many paired birds are recaptured annually in the non-breeding herds to which they have gone to moult or for the winter, thus indicating the regularity of such movements. One female showed an interesting series of movements before pairing, a strong attachment to a particular moulting ground, and a considerable wandering between breeding seasons:

Dec. 1963	1st winter, in flock at Burton-on-Trent.
Jan. 1964	ditto.
March 1964	in flock at Tamworth 11 miles SSW.
June/July 1964	in flock at Stratford-on-Avon 30 miles S.
July 1964	moulting in flock at Cannock 35 miles NNW.
July 1965	moulting in flock at Cannock.
May 1966	paired, nested, hatched three young, Handsworth 11 miles S.
July 1966	moulting in flock at Cannock 11 miles N.
Oct./Nov. 1966	alone at Handsworth 11 miles S.
Jan. 1967	alone at Solihull 8 miles SE.
March 1967	in flock at Stratford-on-Avon 15 miles S.
May 1967	paired, new mate, did not nest, Great Barr 30 miles NNW.
Feb. 1968	paired, same mate, Great Barr.

So strong was her preference for the Cannock moulting ground that in 1966 she deserted her 3 two month old young and left them to rear themselves, which they did successfully. The male bird had been killed in April before the young had hatched.

Breeding success

All the pairs of Mute Swans which nested in the study area were visited at regular intervals throughout the spring and summer to determine their hatching and rearing success and to find the causes of failures. In the earlier years of the study the number of eggs laid and the number of young hatched were not recorded because most of the available time was taken up in locating and catching pairs. However, these data are now being collected and will be reported later in a separate paper.

The percentage of nesting pairs which eventually hatched young has been fairly constant at around 58% over the five breeding seasons 1962 to 1966 (Table XI). It was probably also at a similar level in 1961, when 14 additional nests were not followed to completion, since most of the unsuccessful nests were recorded while it was those which had been sitting for a long period which were omitted. This

Table XI. Hatching success of breeding pairs of Mute Swans.

Year	*Breeding pairs*	*Hatching*		*% of nesting pairs hatching successfully*
		successful	*unsuccessful*	
1961	55	30	25	54
1962	66	39	27	59
1963	55	33	22	60
1964	72	42	30	58
1965	78	52	26	67
1966	68	37	31	54
1967	62	31	31	50

percentage figure includes those pairs which were successful at the second attempt.

Pairs which have lost their first clutch of eggs have been recorded re-laying in all years. It is possible that a few repeat clutches may have been missed in the earlier years. Of 22 pairs which failed in their first nest, 12 (55%) hatched their repeat clutches successfully.

One pair in 1966 had already completed its second clutch by the end of April. Re-laying does not normally take place after early June. However, one pair just outside the study area laid three times one year and still had a single half grown young in mid-December. Another pair laid a repeat clutch in each of the four year it lost its first, but in only one of these years was the repeat successful.

In the study area nearly 80% of nesting failures is due to predation by humans —mainly boys stealing or breaking the eggs (Table XII). Vandalism is particularly marked in the urban areas and while most accessible nests are robbed, those which cannot be reached are bombarded with sticks, bottles, bricks and stones until the eggs are smashed or the parents desert. Some of the failures due to injury or death of one or both of the adults (7% of the causes) are also the result of human persecution. Fortunately if one adult is killed after the eggs have been laid the other adult will often carry on alone and may successfully rear a brood. This is particularly true of females. Breeding birds most frequently meet their death by flying into wires. However, one bird was found dead on the nest apparently eggbound (it had laid a half size egg the previous year), another choked to death on a potato and a third was killed on the nest by a fox. Signs of the immense struggle which had taken place could be traced from the nest, with its scattered eggs, to a point nearly 50 yards away. Groups of feathers showed where the fox had put the dead swan down for a rest on the way back to its den in the woods. It had, however, been unable to lift the bird up a wall at the edge of the field and the body was found there, almost completely eaten. The upper mandible had been bitten off half way along, this presumably being the first hold the fox got on the swan and the one used to drag it away from the nest.

Flooding also causes some nesting failures (8%), particularly of those pairs nesting by streams and rivers. Desertions are rare and in only one case was the cause known. This was when an intruding pair of swans (failed breeders) drove the pair from their nest and territory.

The higher than average percentage of nesting pairs which hatched young in 1965 (67%) was probably due to the relatively inclement weather which kept predatory humans indoors and because the incubation period of most of the pairs was fortunately timed between the Easter and Whitsun bank holidays— peak periods of human predatory activity. In all other years either Easter or Whitsun has tended to coincide with the period when many pairs had eggs. In 1966 the lower than average success rate (54%) was due to the greater opportunities for human predation provided by the very extended breeding season—some birds had full clutches by mid-March, while others were delayed by subsequent cold weather from laying until late April or early May. Losses due to flooding were higher than in any previous year and severe April frosts were thought to be the cause of two clutches failing to hatch—one after being incubated for three months. The very low success rate in 1967 was also due to a combination of a late and extended season and exceptional floods at the end of May.

Table XII. Causes of failure of 192 Mute Swan nests 1961-1967.

Eggs taken or destroyed by humans	*Adult(s) injured or dead*	*Flooded*	*Deserted*	*Infertile*	*Unknown*
150	14	15	5	5	3

Almost all the pairs which hatched eggs subsequently reared at least one young to fledging. Only 12 of 264 broods lost all their young, usually for the same reasons that other broods decreased in size— predation by pike, foxes and humans or as a result of disease or infection. The latter was particularly responsible for the small average brood size of 3.0 in 1964 when many young died in June during a spell of cold wet weather.

The average brood size at fledging over the seven years 1961-67 was 3.5, with the maximum at 4.0 young in 1967. This is slightly higher than the 3.1 found by Perrins and Reynolds (1967). Brood sizes at fledging ranged from one to nine young

Table XIII. Brood size at fledging in the Mute Swan.

Year	*Broods of known size*		*Number of young*									*Total reared*	*Reared per breeding pair*
	No.	*Av.*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*		
1961	23	3.3	4	4	3	8	3	—	1	—	—	—	—
1962	39	3.9	5	4	5	10	9	2	3	1	—	154	2.3
1963	32	3.7	2	5	5	10	5	4	1	—	—	119	2.2
1964	42	3.0	9	9	10	7	4	2	—	1	—	125	1.7
1965	49	3.5	5	12	13	4	9	4	—	1	1	170	2.2
1966	34	3.6	2	8	9	5	5	3	1	1	—	123	1.8
1967	29	4.0	4	5	5	5	3	1	3	2	1	116	1.9
Total	248	3.5	31	47	50	49	38	16	9	6	2	—	2.0

(Table XIII). Two, three and four were the commonest but 13% of the broods were greater than five. One of the two broods of nine young came from a clutch of eleven eggs, ten of which hatched; the other brood came from a clutch of nine eggs. The brood size distribution varied markedly from year to year. Whereas in 1961-63 the commonest brood sizes were four and five, in 1964 they were one to three due to the dying off of many of the young. In 1965 and 1966 two and three were the most frequent sizes but in the former year the average brood size was brought up by the larger than usual number of pairs rearing five or six young as well as by single broods of eight and nine young. In 1967 the warm dry weather throughout June resulted in few young dying after hatching and consequently the brood size was higher than in any other year, and there was an exceptional number of large broods (20% had 7 or more young).

Two examples of young changing from one brood to another have been recorded. In one case a pair occupying a territory on a river and having three half grown young of their own had a fight with an intruding pair of swans. The latter retreated leaving behind their own three young, which were then adopted by the resident pair, which went on to rear all six successfully. The other instance involved one of a brood of five, ringed in its family in September, which was recaptured in another family party three miles away the following January.

Another unusual circumstance occurred in 1966 when a pair, which had hatched young on a remote and rather unsuitable pond, flew off after about a week and left their young to die. It is possible that the desertion was due to the parents' inability to lead their young to more suitable waters. The same thing happened in 1967 but the two young wandered up to a nearby farm where they were fed with the poultry. One adult returned for a short while on each of the next two days but did not stay. The two young were therefore introduced to another family which already contained six cygnets. One was accepted and successfully reared but the smaller one was driven off and perished.

The average number of young reared per breeding pair was 2.0, the same as that found by Perrins and Reynolds (1967), with figures ranging from 1.7 in 1964 to 2.3 in 1962. The total number of young reared to fledging in the study area each year varied from a low of 116 in 1967 to a peak of 170 in 1965. Total production did not correspond closely with average brood size (in fact it was lowest in the year of highest brood size) but depended also on the interaction of the following factors, each of which varied from year to year: (a) total paired population; (b) percentage of the paired population which nested; (c) percentage of pairs hatching young successfully. The good output of young in 1962 was the result of a high average brood size. The very low number of young reared in 1963 was primarily the result of a low paired population and a lower than normal percentage of breeding pairs (Table II) which were not compensated for by an above average brood size. The low production of 1964 was associated with an unusually low brood size due to the dying off of the young in the first few weeks after hatching. The record output in 1965 was due to the combination of a high paired population and an above average hatching success, while the low figure for 1966 came mainly from the poor hatching success. In 1967 the low number of pairs and the very poor breeding success outweighed the effects of the higher than normal percentage of the paired population which nested and the high average brood size to result in the lowest total of young of any of the seven years.

When breeding successes of 13 pairs together for five or more years are considered, we find only 54% of these nests were successful, slightly below the aver-

age for the whole population. This is rather surprising as one might have expected long-standing pairs to have been more successful in repelling human intruders—the main cause of failure.

Two pairs did not rear any young in five seasons. In one of these this was because the female bird was probably infertile due to old age. There is evidence that this pair had been together for many years before the study commenced. The female usually laid only one or two eggs and one of these in each year was only half the normal size. This continued even after it took a new mate in 1966.

One pair reared young in each of the five seasons they were paired together, while another pair reared young in four consecutive seasons after a failue in their first year. The former pair nested on a remote stream and the latter pair in a garden where almost constant watch was kept against egg thieves. Just as human predation is the main cause of nest failures so human protection is the main reason for certain sites being more successful than others, even though one or both of the birds occupying the territory may have changed. Two sites were successful in each of the seven years of the study, two sites in six years and four sites in five of the years.

The breeding success of pairs in which both birds were nesting for the first time (53% of 77) was a little lower than the average for all breeding pairs. There is an indication that new pairs in which at least one bird had bred previously were more successful (66% of 47). The only two birds (both female) which have nested at the age of two were both successful at the first attempt even though both were paired to another bird also nesting for the first time. One laid seven eggs and eventually reared five young while the other reared two young and went on to rear seven young the following year, when it was aged three. Furthermore, both birds of the pair which laid eleven eggs and reared nine young in 1965 were nesting for the first time, but the exact ages of these birds were not known.

Habitat

The habitat occupied by the territories of breeding and non-breeding pairs each year have been divided into five categories (Table XIV). Arbitrary limits, of greater than 10 acres to define large waters and greater than 20 ft. width to define rivers, were chosen. Small waters down to half an acre, the minimum size normally used by swans for nesting, were counted.

An almost equal proportion—more than half—of both the breeding and non-breeding pairs were situated on small waters. The breeding pairs showed rather more preference for streams and large waters, rather less for rivers and canals, than did non-breeders. The main reasons for these differences seem to be in the relative attractiveness of the habitats as breeding sites. Breeding pairs seem to occupy the choicer habitats, such as the clean weed-filled streams, while non-breeding pairs tend to be found on habitats with less suitable feeding and nesting sites, such as the larger polluted rivers.

Table XIV. Comparison of habitats occupied by breeding and non-breeding pairs of Mute Swans 1961-1967.

		Large waters		*Small waters*		*Rivers*		*Streams*		*Canals*	
Status	*Total*	*No.*	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Breeding pairs	470	53	*11*	266	*56*	34	*7*	72	*15*	45	*11*
Non-breeding pairs	190	13	*7*	110	*58*	29	*15*	14	*7*	24	*13*
All pairs	660	66	*10*	376	*57*	63	*9*	86	*13*	69	*11*
Amount of habitat		25 waters		193 waters		128 miles		73 miles		206 miles	

The greater aggressiveness of breeding pairs probably results in a stronger hold on to the more attractive territories for breeding. They also have an advantage in taking up their territories earlier in the spring than non-breeding pairs.

The pattern of site occupation has remained relatively constant over the seven years except that the number of breeding pairs on canals has steadily decreased (from ten to three), due largely to the cleaning out and increased usage of the operational canals and the filling in of the more attractive weed-filled areas of disused canals.

The incidence of pairs in the various habitats also needs to be related to the extent of those habitats in the study area. Thus small waters were eight times as numerous as large waters but only had 5½ times as many nests. So, per water, the latter were more favoured. Again, the mileage of canals was three times that of streams but the latter held more nests. So, per mile, the streams were by far the most utilised. On one stream, the Mease,

there were three nesting pairs on a stretch of seven miles in most years. Another, the Blyth below Blithfield Reservoir, usually had three pairs on four miles. Pairs in these remote country districts were generally the most successful in hatching and rearing young, except when late spring floods washed away nests.

Thirty-eight of the territories have been occupied in at least six of the seven years even though the individuals occupying them have changed several times. Thus over a third of the pairs each year are on traditional sites, most of which, even to the human eye, appear the most attractive for feeding (shallow, weed-filled water) and nesting (reed-fringed margins). The fact that some of these are also particularly susceptible to human predation not surprisingly does not seem to be taken into account by the swans during territory selection. Seven (18%) of the sites occupied in six or more years have never reared young during the seven years of the study.

Many sites in all types of habitat have only been occupied for one or two years. At many of these young have been successfully reared on these occasions, indicating that such territories are suitable for swans. Yet they may remain unoccupied for several seasons. This, together with the fact that only about 38% and 28% of the large and small waters are occupied on an average, seems to indicate that the paired population level each spring has not been primarily controlled by the amount of habitat available.

The future

One of the most interesting features revealed by this study has been the constant level of the paired population each spring during the first six years of the study. Yet the annual output of young has varied widely and the total swan population has decreased by at least 25%. In fact, the highest paired population was probably in 1965, even if allowance is made for a few pairs being missed in the early years of the study. Again, the mortality rate has varied due to two severe winters (one exceptionally so). Such a constant paired population level when so many other factors were varying suggests a habitat availability limitation, and yet there is evidence of suitable habitats remaining unfilled in many years.

The reason for the constancy of the paired population level in 1961 to 1966 therefore remains uncertain at present but the continuation of the study in future years may reveal the answer. There is perhaps already an indication that the decrease in the total population level is at last starting to have an effect on the paired population. There was a significant drop in the number of pairs in 1966 compared with 1965 in spite of a low mortality rate associated with the mild 1965-66 winter. A further indication of the beginning of a downward trend was the lack of new blood in the 1966 breeding population.

It is particularly unfortunate therefore that the oiling disaster at Burton-on-Trent in July 1966 has clouded the picture. It is not clear whether the exceptionally low paired population in 1967 was entirely due to this or in part due to a continued decline from other causes in the number of new birds coming into the paired population which started in 1966. Already by the winter of 1967-68 (18 months after the oiling took place) the size of the Burton-on-Trent flock is back to the normal winter level though the age structure is significantly different from previously. It may therefore be a further year or two before it will become a fully effective reservoir of birds suitable to join the paired population and before the latter's overall trends can be established again. Man has been the primary controller of the swan population level in the past and only time will tell how the various ways in which he is at present influencing the situation will balance out in the future.

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Summary

During seven years, 1961 to 1967, the population of Mute Swans *Cygnus olor* in an area of 550 square miles in the Midlands has been studied intensively by catching and ringing. The present paper deals only with the paired segment of the population. The number of pairs has remained fairly constant, around 95, but there is some evidence of a decrease since 1965. There were annual changes in the proportion of breeding pairs and in the recruitment of new pairs. The swans usually first paired at two and bred at three years old, but there were variations, and the age composition of pairs also had effects on their success. Mortality rates, based on the number of birds found dead, or missing from the area, were around 20% for breeding pairs, 35% for non-breeding pairs. There were other variations in mortality rates related to breeding success as well as to weather. Eighty-five per cent of paired breeders retained the same mate from year to year, if it was still alive. Non-breeding pairs were less stable. Divorce rate was 3% for breeding birds and 9% for non-breeders; some complicated pair histories are described. Movements of paired birds were very circumscribed. Only 58% of nests hatched successfully, human predation or interference being the major cause of loss. Most broods survived in part, with an average size at fledging of 3.5, representing 2.0 young per breeding pair. The production of young from the area varied widely between years, from 116 to 170. The relative attractiveness of different habitats was investigated. Despite the stability of the paired population, much apparently suitable habitat remained unexploited each year.

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