A 39 YEAR STUDY OF A MUTE SWAN *CYGNUS OLOR* POPULATION IN THE ENGLISH MIDLANDS

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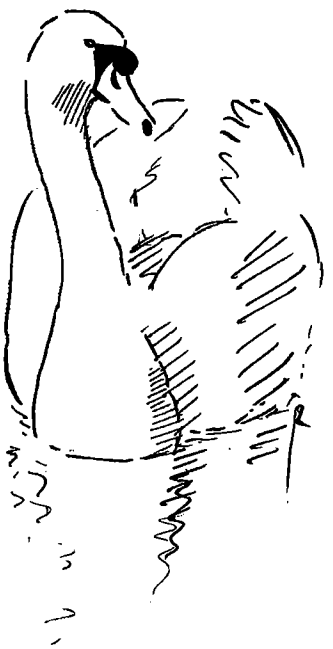

The results of a long-term study of the Mute Swan *Cygnus olor* in a 1440 km^2 area of the English Midlands are presented. During the period 1961 to 1999 the population varied between 213 and 551 birds with the numbers of pairs each spring ranging from 53 to 162. Life histories of 1647 birds marked as cygnets in family parties or in flocks and whose date of death was also known are examined in detail. Of these birds only 11% achieved breeding status, high mortalities occurring in the first two years of life. Approximately 50% of the breeding birds had only one or two breeding seasons and over the period of the study a minority of the breeding adults produced a majority of the cygnets. Most birds were recorded first paired at two or three years old while first breeding mostly occurred at three and four years old. Maximum successful breeding age recorded for both males and females was 18 years. Females showed a higher degree of natal site fidelity and examples of incestuous pairings were recorded, with fertile offspring being produced. The effect of mate and territory change on breeding performance is also discussed. The study illustrates how the parameters affecting population dynamics have varied over a period in which there has been widespread national and marked local fluctuations.

Key words: *Cygnus olor* - life history - breeding success - annual mortality - first breeding - site fidelity

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INTRODUCTION

Long term studies of a species are necessary to obtain critical data, which can then be used to explain population changes. A vast amount of data has been collected during this 39-year study of the Mute Swan *Cygnus olor*. This particular analysis concentrates mainly on data derived from that sub-section of the population for which most information was derived. The monitoring of individual birds from hatching through to fledging, and during their later maturation in non-breeding herds until they eventually pair and breed themselves has enabled valuable information on various aspects of Mute Swan biology to be accrued.

STUDY AREA AND METHODOLOGY

Since 1961, Mute Swans have been studied in a 1440 km^2 area of central England (52°30'N, 2°10'W). Much of the area is rural but there are many large towns and industrialised areas. Three major power stations are associated with river valley systems. River systems and their tributaries offer natural territories for swans, but most territories are man-made and include an extensive complex of canals, several reservoirs and a large number of urban and rural pools of varying size. Over the last 15 years, many additional pools have been provided as irrigation ponds for farms and to accommodate leisure pursuits. Others, particularly in the industrial areas, have been filled in

to accommodate building developments. The commercial extraction of sand and gravel in the area provides extensive tracts of pools, offering potential territories for swans. Many lie dormant for years before being returned to agricultural land; others are retained as landscape features while new pools are continually being produced.

Catching and monitoring methods have been described in previous publications (Minton 1968, 1971; Coleman & Minton 1979) and have continued almost unchanged. Currently, over 95% of birds within the area carry rings. 9370 birds have been ringed since 1961, including 7027 birds ringed as pulli or fledged birds in their first or second year. Of these, 2388 were not seen again after ringing. A further 2992 were recorded on at least one occasion after ringing - 27% even became paired - but eventually disappeared due either to death and remaining undetected or to emigration from the study area. For the remaining 1647 birds, the hatching year and mortality date were both known. These comprised 288 paired birds (136 males and 152 females) and 1359 birds that were never recorded paired. It was this group of 1647 birds which was mainly used in this analysis.

Large individually engraved plastic leg rings have been used since 1969, enabling over 70 000 individual resightings to be made (Ogilvie 1972). Initially, paired birds were sexed by their appearance and behaviour, but since 1979 all birds, irrespective of status, have been sexed cloacally. Recorded mortalities have enabled mortality rates and causes of death to be determined. A pair was defined when two birds were seen to have established and defended a territory. For the purpose of this paper a bird is regarded as being in its first year up to the end of August of the year after hatching. A breeding pair is defined as one that nests and produces eggs; a non-breeding pair holds territory and may build a nest but produces no eggs.

RESULTS

Population changes and cygnet production

The total swan population in the area has been estimated (Minton 1971) by adding the number of paired birds located in spring to the number of unpaired birds remaining in the non-breeding flocks in April. In 1961 the total population was 514 birds. This number decreased to its minimum

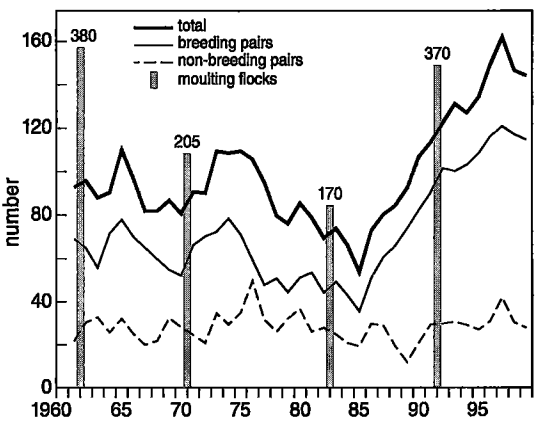

Fig. 1. Annual counts of total number of pairs (thick line), breeding pairs (thin line) and non-breeding pairs (dotted line), 1961-99. Bars and figures indicate counts of moulting flocks in four years.

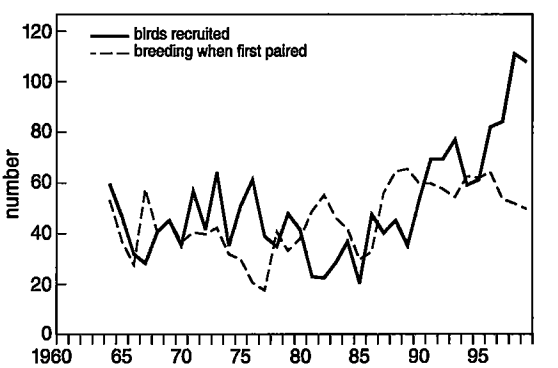

Fig. 2. Recruitment of new individuals to the paired population 1964-99, including number of birds recruited (line) and percentage breeding when first paired (dotted line).

level of 213 in 1985, since when the population level has recovered rapidly, reaching a peak of 551 birds in 1997. Since then there has been a slight decline in the total population. Although summer moulting flocks contain non-breeding and failed breeding birds, including some temporary immigrants which normally reside outside the study area, the total number of birds in moulting flocks show a similar pattern of fluctuations. In 1961 there were 378 birds in the moulting flocks, decreasing to about 170 birds in the mid-1980s and then reaching 525 by 1999.

Annual totals of the paired population (Fig. 1) also show a superficially similar pattern of a decline in numbers to a low point in 1985 followed by a marked recovery to a peak in 1997. However there are some significant differences. For example the total number of pairs remained relatively constant, between 82 and 110 pairs between 1961 and 1976. Only after that year did the marked decline occur to a low of 53 pairs in 1985. The subsequent increase was very rapid reaching a peak of 162 pairs in 1997 - a tripling of the paired population in a period of only twelve years. The paired population has always contained a substantial number of non-breeding pairs. As Fig. 1 shows, the number of such pairs has remained relatively constant, generally between 20 and 35 pairs throughout the 39-year study period. It is the number of breeding pairs that varied most markedly over the period, falling from typically 53-78 pairs in the first 15 years of the study to only 34 pairs in 1985, before climbing rapidly to 120 breeding pairs in 1997. In any one breeding season, the majority of the breeding birds had retained their mate from the previous season and on average 85% of these pairs breed.

The proportion of pairs, which were non-breeding, was typically 25-35% of the total paired population, with a maximum of 44% in 1976 and a minimum of 13% in 1989. Fig. 2 shows how recruitment of new birds to the paired population has increased since 1985 with an average of around 70 new-paired birds each year since 1990. Also, since 1987, the proportion of new recruits, which bred during their first season paired has been at a higher level (around 20%) than previously. The type of territory occupied by paired birds is detailed in Fig. 3. All types of territory have featured in the post 1985 increase in the paired populations. Although 'pools' are the most commonly used habitat and the habitat which has increased most over the last 15 years, only 14 pairs present in both 1997 and 1998 were occupying sites which had been created since 1985. The

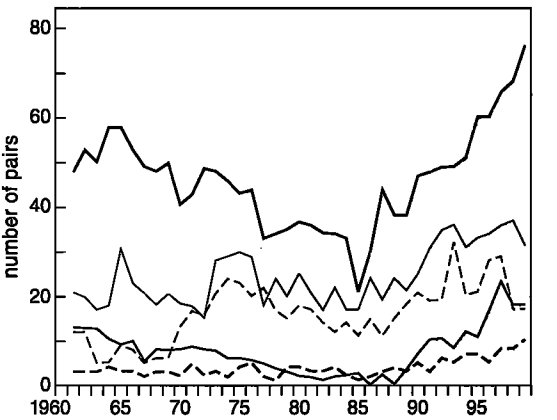

Fig. 3. Number of pairs in different habitats 1961-99. Top to bottom: pools (thick line), rivers (thin line), canals (medium line), gravel pits (thin dashed line), and reservoirs (thick dashed line).

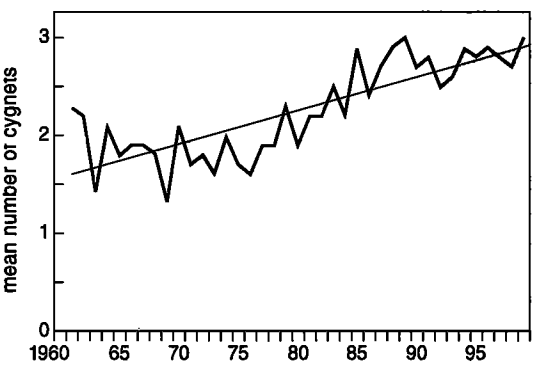

Fig. 4. Average number of fledged cygnets per breeding pair 1961-99, calculated from the number of cygnets alive at ringing, i.e. *c.* 3 months old. The regression line with a slope of 16.6 is highly significant ($r^2 = 0.57$, $P < 0.005$).

number of cygnets fledged per breeding pair is shown in Fig. 4 together with a trend line for change. Over the period 1961-99 there has been a marked increase in productivity, from an average of 1.75 cygnets per breeding pair in the early 1960s to around 2.70 fledged cygnets per breeding pair in the late 1990s. This increased productivity appears to have mainly occurred since the mid-1970s. In absolute terms, the lowest number of cygnets fledged in the study area was 81 in 1969 (followed by 84 in 1979) and the maximum was 341 in 1996.

Annual mortality rates and causes of death

The following analysis is based on the 1647 birds whose year of hatching and death are known. Mortality is measured by the number of dead birds recorded each year expressed as a percentage of the birds alive at the beginning of the year. Table 1 shows the annual mortality rates over the first nine years of life of the 1647 birds, regardless of whether they were 'flock' or paired birds. The mortality rate was almost constant between 27% and 32% throughout this period. This result is surprising given that an increasing proportion of the birds each year were part of the paired population and that earlier work (Minton 1968) showed that mortality rates reduced significantly when birds became paired, especially if they bred and even more so if they bred successfully. The major cause of death was collisions, usually with overhead wires. These formed 30-40% of total deaths and an even higher proportion of deaths where the cause was known.

Analysis of the mortality rates of those birds which were known to have been paired showed that for non-breeding paired birds the average mortality rate was around 30% (range 23-36%) and for those paired birds which were known to be breeding the mean mortality rate was 28% (range 23-40%). These figures further confirm the earlier suggestion that mortality rates of breeding adults now appear to be substantially higher than the maximum of 20% recorded in the previous analysis (Minton 1968).

Among paired birds, as opposed to flock birds, vandalism by man accounted for 6% of deaths for non-breeding birds and 10% of breeding birds, respectively. Among breeding birds, eleven females were shot by vandals, as opposed to five males. Also four males as opposed to one female were killed in territorial disputes with other swans. During the 1970s and 1980s, lead poisoning, from anglers weights, was a major cause of mortality in the English Midlands but within the study area measured lead levels were relatively low, one of the major flocks in the area being used as an unpolluted control by researchers (Simpson

Table 1. Annual mortality of 1647 precisely aged birds during their first 9 years of life and causes of death.

	Year of life								
	1	2	3	4	5	6	7	8	9
Birds alive	1647	1183	804	544	385	282	215	155	112
Birds dead	464	379	260	159	103	67	67	43	34
% Mortality	28	32	32	29	27	24	28	28	30
Causes of death									
Collisions	183	122	90	60	31	21	21	16	7
	39%	32%	35%	38%	30%	31%	35%	37%	21%
Other causes	80	85	62	42	19	15	13	20	10
	17%	22%	24%	26%	18%	22%	22%	47%	29%
Reason not known	201	172	108	57	55	31	26	7	17
	43%	45%	42%	36%	53%	46%	43%	16%	50%

et al. 1979). Only 4% of known causes of death were attributed to lead poisoning but some mortalities of unknown cause were probably also due to lead. Heavy mortality due to oiling of flocks occurred in 1966, 1974 and 1978.

First pairing and first breeding

The total number of males and females in the sample of 1647 birds is not known. In the early years of the study only the paired birds were sexed accurately, the unpaired birds were mostly unsexed and it was only from 1979 that all birds were sexed cloacally. Of the 1647 birds whose date of hatching and death were known, 18% (136 males and 152 females) ultimately paired and 11% (86 males and 91 females) achieved breeding status within the study area. Additional birds presumably attained breeding or non-breeding status outside the study area. To increase this sample, additional birds of known age (but whose death was never subsequently recorded) were included in this section of the analysis. Birds from the smaller sample of known life-span birds paired on average at 3.54 yr (males) and 3.23 yr (females) and first bred at 4.52 yr (males) and 4.16 yr (females). The corresponding values for the larger sample were similar, first pairing at 3.37 yr and 3.23 yr, respectively, and first breeding at 4.21 yr and 4.05 yr, respectively.

A clear and consistent pattern of first pairing and breeding emerged from these data (Fig. 5). Around 60% of males paired at the age of two or three, with a further 31% at age four or five. Females were slightly more precocious with around 68% first pairing at age two or three and a further 25% at age four or five, but this was statistically not significantly different ($\chi^2_7 = 5.2$, n.s.). On average, peak recruitment into the breeding population occurred one year later. Thus only 8% of males were recorded breeding at the age of two. A further 74% of males joined the breeding population in almost equal quantities in years three, four and five. The percentage of females breeding in year two was also 8%, with a slightly higher percentage of birds (78%) joining the breeding population in years three, four and five.

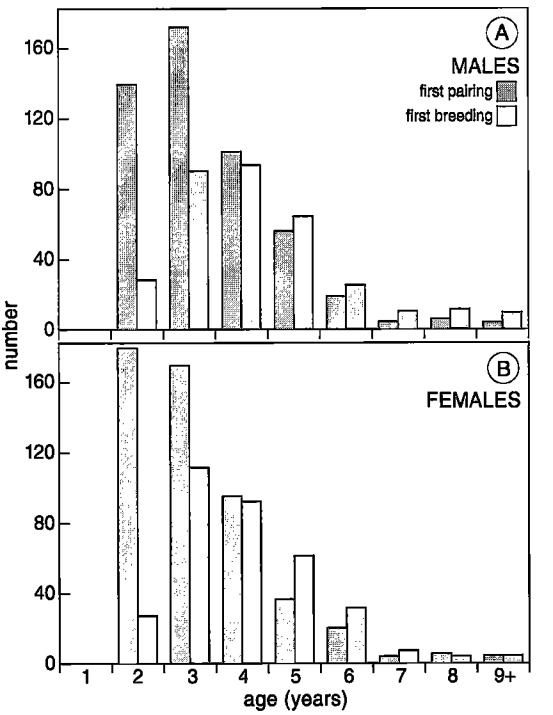

Fig. 5. Age at first pairing (dark grey bars) and first breeding (light grey bars) for (A) males and (B) females.

However the percentage of females which bred for the first time at age three was greater (33%) than the percentage that bred at age five (17%). Again the difference between males and females was statistically not significant ($\chi^2_7 = 5.5$, n.s.).

It is interesting that the proportion of the population first breeding at age two and three appears lower (males 35%, n = 336, females 40%, n = 341) than that recorded earlier in this area (Minton 1968) when the population was lower (males 42%, n = 33, females 52%, n = 27), but this difference was statistically not significant for males and females ($\chi^2_1 = 0.64$ and $\chi^2_1 = 1.34$ respectively). Of the birds that bred in their second year, 54% of males (n = 28) and 52% of females (n = 27) successfully reared cygnets. This is only slightly below the annual rearing success of 59% recorded over the whole period of the study for the whole breeding population. Only one clutch failed to

hatch as a result of infertility - a two year old female was paired to a male at least six years of age who had lost his mate the previous year. Prior to pairing with the young female he had sired 15 cygnets over a six year period. After the initial failure the pair went on to breed for four years hatching only one brood of four cygnets. In all other years the eggs were stolen by vandals.

Natal site fidelity and incestuous pairings

Table 2 shows distances from the natal site of the territories of birds when first recorded as paired or breeding. 33% of males and 50% of females took up territories within five kilometres of their birthplace. This difference between the sexes is significant (χ^2_2 = 17.9, P < 0.001). Seven records of incest were noted (Coleman *et al.* 1994): mother/son (n = 3), father/daughter (n = 1), brother/sister from the same brood (n = 3). All parent/sibling pairings were recorded on the natal site and in each case the other parent was recorded dead or missing during the previous winter. Also two of the brother/sister pairings each from the same brood, were recorded on the natal site after both parents had been killed. Of all breeding attempts recorded by incestuous pairs most, (70%, n = 26) produced no young. However there were examples of breeding success in all three, with a total of eleven nesting attempts producing 46 cygnets of which 39 were reared. These were derived from one mother/son pairing rearing 18 young in three breeding seasons, one father/daughter pairing rearing eight cygnets in two breeding seasons and one brother/sister pairing rearing thirteen cygnets in four breeding seasons. Interestingly, in all cases the hatching and rearing success of each successful pair was higher than the average hatching/rearing success calculated for the year as a whole. Three of these cygnets themselves subsequently bred successfully (two males and a female), hatching a total of 17 cygnets, of which 15 fledged. A further three of the cygnets paired but did not breed.

Table 2. Percentages of males and females settled at various distances from their natal site when first seen paired or breeding. Included are also birds of known age, but still alive.

Distance from natal site	Males (n = 222)	Females (n = 243)
0-5 km	32	51
6-15km	34	28
> 15 km	34	21

Life span of paired birds and length of paired breeding life

Of the 288 birds (136 males and 152 females) which paired during their life, 60% of males and 58% of females survived beyond their fifth year and 16% of males and 11% of females survived beyond their tenth year (Fig. 6). Only six (4%) males and seven (5%) females survived to an age greater than 15 years. There was no significant difference in lifespan between male and female paired birds. The maximum recorded age for a female was 19 and for a male 18 years. The length of time for which birds remained paired is shown in Fig. 7. The pattern is similar for both males and females. The duration of the paired life was only one or two years for 50% of males and 53% of

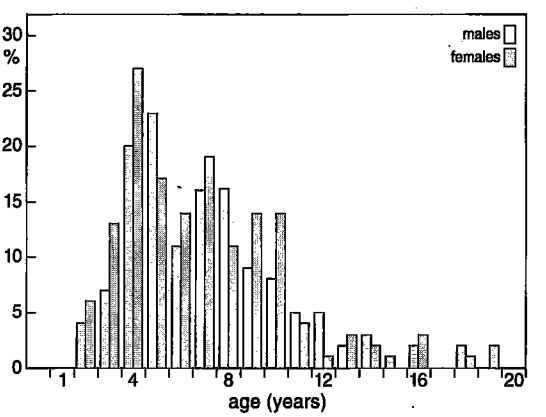

Fig. 6. Lifespan of paired males (n = 136, mean 7.32 yr) and females (n = 152, mean 7.00 yr) of known hatching and mortality date. The frequency distributions of males and females are not significantly different (χ^2_{10} = 8.2, n.s., for ages 2 - 11, > 11).

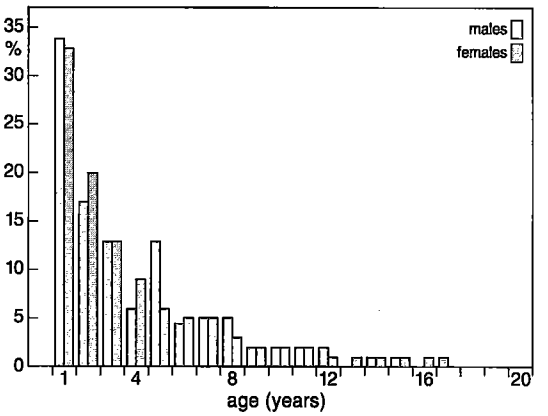

Fig. 7. Length of paired life in males (n = 108, mean 3.93 yr) and females (n = 105, mean 3.78 yr) of known hatching and mortality date. The frequency distributions of males and females are not significantly different ($\chi^2_8 = 4.0$, n.s., for ages 1 - 8, > 8).

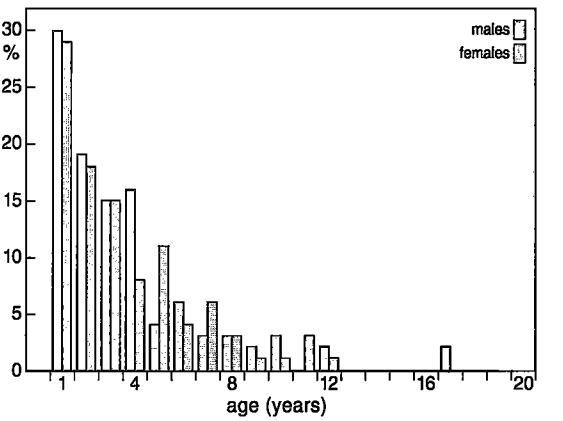

Fig. 8. Number of breeding seasons of paired breeding males (hatched, n = 105, mean 3.66 years) and females (black, n = 100, mean 3.51 years). The frequency distributions of males and females are not significantly different ($\chi^2_7 = 7.8$, n.s., for ages 1 - 7, >7).

females. This was principally due to mortality but a small number of birds, which lost their mate, did not pair again before ultimately succumbing themselves. However, 21% of males and 19% of females remained paired for more than five years during which time 65% of the males and 64% of the females changed their mate at least once. Only 7% of males and 5% of females remained paired for more than ten years. The maximum paired life was 16 years for a female and 17 years for a male during which time the female changed her mate three times and the male twice.

Of the paired birds, 37% of males and 40% of females were never recorded breeding. Table 3 gives details of their paired life. 92% of both males and females were only part of a non-breeding pair for one or two seasons. Since 70% of males and 82% of females were first paired at two or three years old, most of these non-breeding paired birds were youngsters. However, four males and five females paired for three or more seasons and one male retained his mate for three seasons. In all other cases, changes of mate and/or territory occurred. No significant difference in length of paired or breeding life between males and females was noted. Poor condition may be a factor preventing breeding success in some individuals since the mates of three females and one male achieved breeding status with other birds. The fact that many established breeders have successful breeding seasons after mate changes may also suggest poor condition being responsible. It is also possible that in some cases incompatibility rather than condition may play a major role in preventing breeding success. The longest continuous non-breeding span, after pairing, was seven years for a male and four for a female.

Of the paired birds, 63% (n = 136) of males and 60% (n = 152) of females were, or eventually

Table 3. Number of years for which non-breeding birds were paired. The figures given are percentage distributions of males and females.

Number of non-breeding seasons	Males (n = 50)	Females (n = 61)
1	72	61
2	20	31
3	4	3
>3	4	5

became, breeding birds (Fig. 8). 49% of breeding males and 48% of breeding females only bred for one or two seasons during their lives. Only 16% of males and 18% of females survived for more than five breeding seasons. Only two males (2%) and three females (3%) survived for more than ten years after first becoming breeding birds. One male survived for 17 breeding seasons but the longest period for a female was twelve seasons. The life cycles of breeding males (n = 86) and breeding females (n = 91) can be classified into three categories. (1) Birds which bred continuously throughout their paired life. 31% of all breeding males and 38% of females fell into this category. The longest period of continuous breeding was 17 years for a male and eleven years for a female. (2) Birds that had non-breeding seasons dispersed among breeding seasons. 22% of males and 16% of females were in this category. In most cases non-breeding was associated with mate change and presumably was mainly because the new mate was not in suitable condition or mature enough to breed (see change of mate or territory below). (3) Birds which had non-breeding seasons either at the beginning or the end (or both) of an otherwise continuous breeding span. 47% of males and 46% of females were in this category. The majority (55% of males and 65% females) had non-breeding seasons only prior to the breeding span. As indicated earlier, it was almost the norm for a bird to have at least one paired non-breeding season before becoming part of the breeding population. However 17% of males and 27% of females had non-breeding seasons at both ends of the breeding span while 28% of males and 5% of females had non-breeding seasons only at the end of the breeding span. This suggests that some individuals may survive to an age beyond which breeding can occur either because of loss of fertility or inability to secure a suitable territory. Interestingly, only 33% of the males (n = 12) that had non-breeding seasons only at the end of a continuously breeding span remained on their territories as non-breeders until death. In contrast, of two females recorded in the same category, one remained on her territory as a non-breeder until death, the other returned with her mate to a non-breeding flock after her last breeding season.

Cygnet productivity and retention of reproductive capability

Cygnet production by 177 breeding birds, which form the basis of this detailed analysis, appeared to be similar for both sexes and the data was therefore combined in Table 4. There was a wide spread in lifetime productivity between individual breeding birds. 22% did not produce any fledged cygnets and a further 26.7% produced only 1-5 fledged cygnets during their breeding lives. In contrast 5.6% of breeding birds reared 21-25 cygnets during their lifetime and 6.8% of the adults produced more than 26 cygnets. The maximum number of cygnets reared by a male during its lifetime was 41 and by a female 50. 20% of the breeding adults produced 59% of the fledged cygnets over the 39-year period of the study. Such wide variation in life time breeding success is typical of many long lived bird species, i.e. a minority of the breeding adults produced a majority of the young (Newton *et al.* 1989).

High lifetime productivity was, however, not solely dependent upon the number of years in which a bird bred. For example three birds each producing 16 fledged cygnets took, three, seven and twelve seasons respectively to achieve this. Similarly, while one bird produced 50 fledged cygnets over an 11-year breeding period, another produced only 19 in a similar period. In contrast,

Table 4. Number of cygnets produced by breeding individuals (n = 177).

Number of cygnets produced	Percentage of breeding individuals
0	22.7
1-5	26.7
6-10	18.8
11-15	11.9
16-20	7.4
21-25	5.6
> 25	6.8

one bird bred for seven seasons and produced two fledged cygnets; another bird bred for eight seasons and produced three fledged cygnets.

A number of birds were recorded paired for at least ten years. In females, the maximum age recorded producing fertile eggs was 18 years (n = 1). Other females produced fertile eggs at 12 (n = 1), 13 (n = 1), 15 (n = 2) and 16 years of age (n = 2). In males the maximum age recorded successfully fertilising eggs was also 18 years (n = 1). Other males successfully fertilised eggs at 12 (n = 1), 13 (n = 2), 14 (n = 2) and 17 (n = 1). An extreme example of probable infertility by one or possibly both of a pair occurred in two birds which were paired together for 15 years. They never hatched any young although eggs were laid in seven breeding seasons. In four of these seasons the eggs were incubated well beyond the normal incubation period. In each clutch one egg was considerably smaller than the norm.

Change of mate and territory in breeding birds

40% of males and 42% of females kept the same mate and territory throughout their breeding lives (Table 5), but 50% of these males and 58% of these females only bred for one or two seasons. The remaining birds changed either their mate (males 23%, females 21%), territory (males 10%, females 11%) or both, either simultaneously or on separate occasions (males 27%, females 26%) at least once during their breeding life.

When only a mate change was involved, divorce (38% of males and 36% of females) was responsible for a surprisingly high proportion of the changes. Death (17% in males and 11% in females) was the other known main cause of mate change and it is likely that most of the other 'unknown' causes were due to death. In most cases taking a new mate resulted in no immediate change to the breeding status, with 59% of males and 63% of females continuing to remain as breeding or non-breeding paired birds with their new mate. However some birds did change their breeding status. As a result of mate change, 19% of males and 37% of females changed from non-breeding to breeding status. The remaining 22% of males changed from being breeding to non-breeding birds. 50% of the birds that changed their territory while retaining their mate did so after experiencing a season as a non-breeding pair on their original territory. A further 27% changed territory after failing to breed successfully. The remaining birds (three males and three females) changed their territory, even though they had bred successfully in the previous breeding season. In birds which changed both mate and territory, not necessarily simultaneously, divorce was the major known cause of mate change (50% males and 42% females). As for territory changes not associated with mate change, many birds which changed territory experienced a concurrent improvement of status (29% of males and 31% of females) from paired non-breeders to paired breeders. Irrespective of whether the change was in territory, mate or both, overall results of changes showed 63% of females and 50% of males did not change their status in

Table 5. Instances of change in mate and territory in 177 breeding birds whose hatching and death dates were known. Given are the percentage distribution of males and females and the mean number of cygnets produced per bird.

	Males (n = 86)		Females (n = 91)	
	%	cygnets bird^{-1}	%	cygnets bird^{-1}
No change of mate or territory	40	7.8	42	4.6
Mate change only	23	7.1	21	10.4
Territory change only	10	2.6	11	4.9
Mate and Territory change	27	10.5	26	10.7

the following season. A further 30% of females and 35% of males went from non-breeding to breeding status, while the remaining 7% of females and 15% of males went from breeding to non-breeding status. Divorce did not always follow failure to breed successfully.

DISCUSSION

The marked increase in population size within the study area after the mid-1980s followed the national pattern (Delaney *et al.* 1990). Whilst these national changes are thought to be closely associated with the prohibition of lead weights used by fishermen, this study suggests that locally other factors may be involved too. The decline in population size in the study area was accelerated by three major oil spills in 1966, 1974 and 1978 which almost totally wiped out some of the non-breeding flocks (Minton 1978; Coleman *et al.* 1991). These flocks, which act as a source of recruitment to the breeding population, took some years to recover. Also, vandalism of nests, particularly in the industrialised parts of the study area, were particularly rife in the early years, leading to reduced breeding success (Coleman *et al.* 1991). Furthermore, the lead levels measured in Mute Swans in the Tamworth area was in fact much lower than in many other areas in the Midlands sampled by research workers (Simpson *et al.* 1979).

The most tangible cause of the increased population in the study area has been an increase in the average number of fledged cygnets produced per breeding pair. This is considered to be partly due to the increase in protection provided by members of the public and conservation organisations. It is also possible that a contribution to the productivity increase has derived from a better fitness level in birds as a result of reduced lead levels, milder winters and a possible improvement in water quality (and consequently food availability). Higher survival due to mild winters also enables pair bonds to remain intact. The ubiquitous and sustained feeding of bread and grain to all sections of the Mute Swan population within the study area may also help to reduce mortality and increase breeding productivity.

The population increase and the concomitant increase in paired birds does not appear to be markedly associated with the increased amount of breeding habitat now available. Nor does it appear that the increased number of pairs and total cygnet production is resulting from birds pairing or breeding any earlier in recent years than they did in the early years of the study - in fact the reverse is true. A puzzling feature of the analysis of this particular segment of the population (those whose year of hatching and death are both known), is that the annual mortality rates seem to be almost constant over the first nine years of life. Earlier studies (Perrins & Reynolds 1967) indicated that birds in their first or second year of life, especially when they were still part of a non-breeding flock, exhibited a significantly higher level of mortality than older birds, especially when the latter reached paired or breeding status. The current study suggests that the mortality rates of flock birds are now rather lower than previously, whilst that of paired or breeding birds is somewhat higher than before. Given that flying into obstacles is still the main recorded cause of death, and no reduction in such obstacles is apparent, it is unclear why mortality rates should have changed in the way they have. It seems possible that the reduction in mortality in flock birds may, over and above any contribution from reduced lead poisoning, be associated with the generally milder winters over recent years. There were three very severe winter periods between 1961 and 1985 during which the population suffered its long decline. There have been no winter periods of equivalent severity in the study area since 1985. There have also been no serious oil spills or other pollution incidents in recent years.

It is interesting that the population seems to have levelled out, or even declined slightly, since 1997. It will therefore be valuable to continue to monitor in the future the various parameters which contribute to the population dynamics of Mute Swans in this study area.

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REFERENCES

Coleman A.E., C.T.D. Minton 1979. Pairing and breeding in Mute Swans in relation to natal area. Wildfowl 30: 27-30.

Coleman A.E., C.D.T. Minton 1980. Mortality of Mute Swan progeny in an area of south Staffordshire. Wildfowl 31: 22-28.

Coleman A.E., C.D.T. Minton & J.T. Coleman 1991. Factors affecting the number of pairs and breeding success of Mute Swans *(Cygnus olor)* in an area of south Staffordshire, England between 1961 and 1985. In: Bacon P.J. & J. Sears (eds). Proc. Third IWRB International Swan Symposium, Oxford 1989. Wildfowl 1991, Supplement 1: 103-110.

Coleman J.T., A.E. Coleman & D. Elphick 1994. Incestuous breeding in the Mute Swan. Ringing & Migr. 15: 127-128.

Minton C.D.T. 1968. Pairing and breeding in Mute Swans. Wildfowl 19: 41-60.

Minton C.D.T. 1971. Mute Swan blocks. Wildfowl 22: 71-88.

Newton I. (ed.) 1989. Lifetime reproduction in birds. London, Academic Press.

Ogilvie M.A. 1972. Large numbered leg bands for individual identification of swans. J.Wildl. Mgmnt 36: 1261-1265.

Perrins C.M. & C.M. Reynolds 1967. A preliminary study of the Mute Swan. Wildfowl 18: 74-84.

Simpson V.R., A.E. Hunt & M.C. French 1979. Chronic lead poisoning in a herd of Mute Swans. Env. Poll. 18: 187-202.

SAMENVATTING

De resultaten van een langetermijn-onderzoek naar de Knobbelzwaan *Cygnus olor* in een 1440 km^2 groot onderzoeksgebied in midden-Engeland worden gepresenteerd. Gedurende de onderzoeksperiode, van 1961 tot 1999, varieerde de populatie van 213 tot 551 vogels, met een jaarlijks aantal broedparen in ieder voorjaar variërend van 53 tot 162. Gedetailleerde 'levensbeschrijvingen' van 1647 zwanen die als kuiken waren geringd in familiegroepen of in andere concentraties Knobbelzwanen en waarvan ook de sterfdatum bekend was, werden in detail bestudeerd. Van deze zwanen bereikte slechts 11% ooit de status van broedvogel en de hoogste sterfte werd gevonden gedurende de eerste twee levensjaren. Ongeveer de helft van deze broedvogels nam slechts een- of tweemaal deel aan een broedseizoen en uiteindelijk zorgde een kleine minderheid van de gevolgde zwanen voor de overgrote meerderheid van de in deze populatie geproduceerde jongen. De meeste broedvogels vormden na twee of drie jaren een paar, maar kwamen pas na drie of vier jaar daadwerkelijk voor het eerst tot broeden. De hoogste leeftijd van een succesvolle broedvogel bij zowel mannetjes als vrouwtjes was 18 jaar. Wijfjes vertoonden een grotere neiging tot trouw aan de broedplaats dan mannetjes en verschillende voorbeelden van incestueuze paarbanden werden gevonden, waaruit overigens vruchtbare nakomelingen voortkwamen. Het effect van verandering van partner en/of nestplaats op de broedresultaten wordt in dit stuk eveneens belicht. Het onderzoek illustreert hoe bepaalde parameters die de populatiedynamica beïnvloeden, in de loop der tijd kunnen variëren. (CJC)

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