Measurement of the demographic parameters of the Mute Swan *Cygnus olor* population in the Lothians

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Abstract

The Mute Swan population in the Lothians has been studied since 1978. Only 15 pairs bred at that time in the study area (2,000 sq km); however, this figure increased to 55 pairs by 1993 which represented a mean annual increase of 9% per annum. The breeding population comprised 39.8% of the total population in April during the period 1978 to 1985; a decrease, to 33.9%, occurred in this proportion during the period 1986 to 1993. The aim of the study was to determine the extent to which the increase in the number of breeding pairs was due to high productivity in the Lothians, or if it was due to immigration.

Adult swans and cygnets which hatched in the study area were marked with individually numbered Darvic leg rings and the sex of cygnets was determined at the time of ringing. A mean of 76.5% of cygnets which fledged each year were colour ringed between 1982 and 1993.

Up to 70% of small cygnets fledged with a mean of 2.7 cygnets fledged per breeding pair but only 1.4 cygnets fledged per breeding pair which included a philopatric female. Productivity was lower on rivers than on canals or still waters. Low productivity was a feature also of low altitude still waters where 2.1 cygnets fledged per breeding pair due to a high cygnet mortality rate of 43%. Biometric data indicated that the proportions of males and females at fledging were equal.

The survival rate in the first year after fledging was 70%

which was lower than in the subsequent nine years. There was no significant difference in the survival rates of males and females during the first six post-fledging years. The age at which swans bred for the first time ranged from 2 years to 7 years for both sexes and no significant difference was detected in the mean age at first breeding between males (3.7 years) and females (4.3 years). In addition, the age-specific number of swans which survived to breeding age was estimated.

Mean annual mortality in the breeding population was 14.3% with no significant difference between males and females. There was a net loss to the breeding population of 6.4% males and 5.2% females due to established breeding birds permanently leaving the breeding population. The percentage of immigrants in the breeding population and the percentage of swans hatched in the Lothians which emigrated to other breeding populations or never bred were estimated also.

A model of the breeding population was formulated using demographic parameters estimated during this study. From this model it was established that the intrinsic segment of the breeding population in the Lothians was able to sustain its numbers through its own productivity. However, the breeding population was dependent upon immigration in order to achieve a mean annual increase in excess of 2%. Productivity from some breeding territories was sufficient to maintain stability in the intrinsic breeding population while productivity from others was not. Breeding territories from which poor productivity was recorded were dependent on excess productivity from the over

productive territories and on immigration for persistent occupation by breeding pairs. This may have inhibited the rate of increase in the number of breeding swans in the Lothians.

It is shown that determination of a critical value for each demographic parameter is of little value. The need for long term continuous monitoring of a Mute Swan population is stressed, as is the measurement of all demographic parameters, in order to make a realistic assessment of a population's ability to maintain the size of its intrinsic breeding population.

Chapter 1

Introduction

The dynamics of animal populations is effected by a number of demographic parameters, including productivity, mortality and immigration. An understanding of population dynamics depends upon measurement of these parameters in order to explain gains or losses in species numbers. Assessment of these parameters through fieldwork is frequently constrained by time and resources and has led to the development of many theories on population dynamics. Theory is a poor substitute for fieldwork, particularly when flawed conclusions may be applied to the management of pest species and conservation or restoration of endangered species. The Mute Swan is a good model species to study since its demographic parameters can be determined more readily by fieldwork than is possible for many other species.

The Mute Swan *Cygnus olor* is primarily a species of the Palearctic where numbers are estimated to be 500,000 individuals, including 49,000 breeding pairs (Wieloch 1991). Distribution, although not continuous, extends from France through north-central Europe, including countries bordering the Baltic Sea, areas around the Caspian and Black Seas, through to China (Cramp and Simmons 1977). Introductions have been made to North America, Australia, New Zealand and South Africa.

The British population, including some 4,000 breeding pairs, is part of the almost continuous west and central European population which in turn constitutes the major part of the European population numbering 28,400 breeding pairs in the late 1980's (Wieloch 1991). There has been an increase in the number of birds in the European population and expansion in its range since the 1970's (Earnst 1991).

The western and central European population used to be divided into seven sub-populations (Atkinson-Willes 1981). However, this number was reduced (Monval and Pirot 1989; Wieloch 1991) following the combination of the three British sub-groups, England and Wales, Scotland and Orkney, and the Outer Hebrides, to produce five sub-populations namely, 1.Scandinavia-Baltic 2.Netherlands 3.Central Europe 4.Ireland 5.Britain.

These sub-populations were not isolated from each other since, by 1993, forty nine birds ringed in Britain had been found abroad and thirteen birds ringed abroad had been found in Britain (Mead et al. 1992; Mead et al. 1993; Mead and Clark 1993). The countries involved, all located within the above five sub-populations, were the Baltic States, Sweden, Denmark, Germany, Netherlands, Belgium and France. In addition a number of swans ringed in the Outer Hebrides were reported in Ireland (Chris Spray pers comm.). Within that group of countries long-term studies and colour ringing of individual swans had been undertaken in Sweden, Denmark, Netherlands, and Ireland. Since the present study is a long-term study, 1978 to 1993, and a large proportion of the data were generated through colour ringing, results from the Lothians will be compared primarily with results from studies in Sweden, Denmark, Netherlands, and Ireland.

Sweden

Mute Swans have bred in eastern Sweden since the 17th century but not on the west coast until the 1930's. A study of moulting birds, including ringing, commenced in the 1960's. By 1979 a considerable increase had occurred in the number of breeding pairs on the west coast (Mathiasson 1981a).

Denmark

Excessive hunting had reduced the Danish population to 3-4 breeding pairs in 1924. Legal protection was introduced in 1926 and by 1981 the breeding population numbered 4,000 pairs (Bacon and Andersen-Harild 1989). Colonial breeding developed as the breeding population increased. Prior to 1900 colonial breeding was unknown; between 1943 and 1957 1-2% of pairs bred colonially, increasing by 1966 to 650 pairs in 25 localities and by 1978 to 1,500 pairs representing 38% of the breeding population (Bacon and Andersen-Harild 1989).

Studies of the breeding populations in Copenhagen and North Sjaelland commenced in 1966 and ringing began in 1967. The project was expanded in 1971 to include colonial breeding birds in the Roskilde Fjord. There was little change in the number of breeding pairs in the Copenhagen population by 1983 while the Roskilde Fjord population increased substantially (Bacon and Andersen-Harild 1989).

The Netherlands

The Netherlands population was described by Esselink and Beekman (1991) as endemic. Archaeological excavations of waste pits uncovered remains which indicated that Mute Swans were hunted in that country 2,000 years ago. The species was semi-domesticated in the Middle Ages when its meat and down were economically valuable. Although swan farms were established, hunting continued and by the beginning of the twentieth century virtually no wild Mute Swans remained. Legal protection from hunting and nest destruction was introduced in 1936; the last farm had closed by 1948. Breeding numbers increased from only one pair in 1948 to 2,500 in the 1970's, then 3-4,000 in the mid 1980's, remaining stable from 1984 to 1989 (Esselink and Beekman 1991).

Esselink and Beekman (1991) calculated that 20-25% of the Dutch population were legally shot and 30-40% of nests were disturbed each year during the 1980's in order to reduce the size of the population and reduce damage to crops; culling continued to be practised up to 1995 (Beekman pers comm.). A study of the breeding population in the Groningen area of north-east Netherlands commenced in 1984 where the number of breeding pairs increased between 1984 and 1989 (Esselink and Beekman 1991).

Ireland

Introduced swans were present in Cork in the early 1700's and found in captivity elsewhere in Ireland (O'Donoghue et al. 1992). It had been presumed that the spread of the species in Ireland during the past one hundred years had been due to introductions; however, Collins and Whelan (1990) argued that a reduction in persecution was responsible for the increase, as had occurred in the Netherlands and Denmark. As a result of genetic studies, O'Donoghue et al.(1992) suggested that the population might be less isolated than previously thought.

The Irish population was estimated to be 5-7,000 birds

(Ogilvie 1972a) and that figure remained the best estimate available to Keane and O'Halloran (1992). Population censuses had been too infrequent to establish a population trend (Smiddy and O'Halloran 1991). Wieloch (1991) gave an estimate for the breeding population as 1,000 pairs.

A study in the Dublin area, including ringing, commenced in 1983 (Collins 1991). The study area covered 1,350 sq km and centred on the city of Dublin. There was no evidence of lead poisoning. No trend in the size of the population has been described.

The breeding population in an area of 370 sq km in southeast Cork has been studied since 1972 (Smiddy and O'Halloran 1991). The number of breeding pairs was recorded in 1987, 1988 and 1989 and there was little variation in totals for each year. No attempts were made to estimate the total number of birds in the population thus no reliable population trend was established either.

Lead poisoning due to the ingestion of discarded lead fishing weights and spent shotgun pellets was investigated in Ireland between 1983 and 1986 by O'Halloran et al. (1991) who found that 68% of the dead swans examined in their study had died from lead poisoning.

Britain

Mute Swans were present in Britain and widespread in England prior to 1250 (Bannerman and Lodge 1953; Ticehurst 1957). They were highly valued as a food source and consequently during the mediaeval period the population was reduced to a semi-captive state. The Crown granted swan ownership rights to landowners in England and the history of this custom was described by Birkhead and Perrins (1986). A history of swan-upping on the River Thames in

London, in addition to swan counts on the river dating back to 1823, appeared in Cramp (1972). In Scotland the swan was not a royal bird, although it was valued as a food source and in 1551 the Scots Parliament passed an Act to fix the price of a swan at five shillings each (Baxter and Rintoul 1953).

Linlithgow Loch was reported to have held Mute Swans in the time of Charles I (Baxter and Rintoul 1953) and an introduction was made to Duddingston Loch by the Duke of Lauderdale in 1678 during the reign of Charles II (Kirke Nash 1935). As in England, the species became semi-domesticated in Scotland and was introduced to many lochs throughout the country up to the end of the last century (Baxter and Rintoul 1953). It is only in the last one hundred years that the British population has returned to the wild state (Birkhead and Perrins 1986).

The species was fairly abundant in Midlothian in the 1930's (Kirke Nash 1935). Bannerman and Lodge (1953) and Baxter and Rintoul (1953) reported the Mute Swan as a common breeding bird in Scotland, although uncommon in the north-west Highlands and absent from Banff, Caithness and Skye. Results from the breeding bird atlas 1968-1972 indicated distribution in Scotland was widespread, apart from unsuitable upland areas (Sharrock 1976). Breeding was not recorded on the Shetland Islands or on Lewis during that time, although they were by then breeding in Banff and Caithness. A decade later, breeding had still not been recorded on Lewis, Harris and Skye, although the odd record had been collected on Shetland (Thom 1986). Thom (1986) reported scattered records of birds present, but not breeding, from Fair Isle, St. Kilda and the Isle of May and the first occurrence on Lewis in 1974.

Censuses of the British population

There have been four national censuses of the British population and one partial census of England and Scotland.

1955-56

The results of the first census, which commenced in 1955 and was partially repeated in 1956, showed the population to number 19,000 birds (Rawcliffe 1958; Campbell 1960). This figure was later adjusted, to take into account poor coverage in some areas of the country, by Ogilvie (1981) to 19,900-21,600 birds which included 3,500 nesting pairs.

1961

A partial census in England and Scotland was instigated in 1961 in order to assess claims that excessive numbers of swans had caused unacceptable crop damage. Results indicated no marked increase had occurred since 1955 and that crop damage by swans was localised; the population was about 19,000 birds (Eltringham 1963). The English population sustained considerable losses during severe weather in the 1962-63 winter (Boyd and Ogilvie 1964; Ogilvie 1967).

1978

The 1978 census was organised to determine if the substantial population decline detected in some areas of England was reflected nationally. Results indicated a national decline of up to 15% compared with numbers in 1955; the total population numbered 17,800 to 18,400 birds including some 3,115 breeding pairs (Ogilvie 1981).

1983

By the late 1970's lead poisoning had been established as a major cause of swan deaths in the south of Warwickshire (Hardman and Cooper 1980) and on the River Thames (Birkhead 1982). It was estimated that in England 2,000-2,500 birds, or 15% of the population, and 700-1,000 cygnets died each year from lead poisoning (NCC 1981). A census was held in 1983 to monitor the national situation. Although the total population had increased by 7% since 1978 and numbered 18,750 birds, including 3,150 breeding pairs, it was still lower than in 1955-56 (Ogilvie 1986).

1990

Following a ban on the sale of lead fishing weights in England and Wales in 1987 a further national census was organised in 1990 in order to assess the effect of the ban. A preliminary report indicated the population numbered 25,748 birds including 3,973 breeding pairs (Delany et al. 1992); the final report has not been published.

Sears and Hunt (1991) found a significant decrease in the number of swan deaths due to lead poisoning in England in the period 1987-1988, although lead poisoning continued to be a major cause of mortality because many weights, discarded before the ban, continued to be accessible to feeding swans.

Censuses of the Scottish population

The 1955-56 census of swans in Scotland was organised by Rawcliffe (1958). The population was estimated to be 3,054 birds including 463 breeding pairs but, following some adjustments for poor coverage, this figure was rounded up to 3,500-4,000 birds by Ogilvie (1981) who estimated 3,680 birds, including 665 breeding pairs, in Scotland during the sample census in 1978. By 1983 the population numbered 3,250 birds including 564 breeding pairs (Brown and Brown 1985). The 1990 census recorded a population of 4,992 birds including 828 breeding pairs; this represented a 59% increase since 1955-56 and a 65% increase since 1983 (Brown and Brown 1993).

Studies in Britain

Abbotsbury

Swans at Abbotsbury, Dorset, were managed in the past to provide food for the estate (Perrins and Ogilvie 1981). Records relating to the swannery date back to 1393 and some management techniques persist. It is situated on the Fleet, a tidal lagoon about 14 km in length which varies between 100 and 1,000m in width, in Dorset. Swans nest in a single colony and nesting material is provided. They nest in close proximity (as close as 2-3 m) and are not aggressive to their neighbours. Cygnets which hatch first are placed with their parents in small pens and cygnets which hatch later are removed from their parents and added to the pens until each pen holds 15-20 cygnets. Food is provided until their release in September.

A detailed study of swans at Abbotsbury and nearby Radipole Lake, a fresh water lake some 10 km distant from Abbotsbury and 1 sq km in size, commenced in 1968 and a colour ringing programme began in 1977 (Perrins et al. 1994). From 1969 to 1980 there was no overall increase in the total number of swans counted annually in May, or in the total number of breeding pairs (Perrins and Ogilvie 1981). An increase in the number of breeding pairs occurred during the period

1969 to 1993 (Perrins et al. 1994).

South Staffordshire

The long term study of the population in South Staffordshire, covering 1,440 sq km, commenced in 1960 and included ringing. The area is generally rural except for the industrial area of Birmingham and Wolverhampton. Habitats frequented by swans include streams, small pools resulting from coal mining subsidence, gravel pits and large lakes in private estates. Canals tended to be polluted by industrial waste as were a number of rivers (Minton 1968). During the period 1961 to 1966 there was a 33% decrease in the number of non-breeding birds while the number of breeding pairs was fairly constant (Minton 1968). The total population declined by 40% between 1961 and 1971, although there was no general change in the number of breeding pairs (Minton 1971; Coleman et al. 1991). However, by 1985 a substantial decline had occurred also in the number of breeding pairs (Coleman et al. 1991).

Oxford area and the lower River Thames

Perrins and Reynolds (1967) commenced a study of swans in the Oxford area in 1960. The study area, centred on Oxford, included almost 100 km of the River Thames plus tributaries. During the period to 1982 the population remained fairly stable while the lower Thames population declined (Birkhead and Perrins 1985) although Bacon (1980) indicated that the number of breeding pairs declined from about 100 in the early 1960's to 70-80 by 1978. Ringing was undertaken, but not continuously, throughout the study area.

Wylye Valley

The valley of the River Wylye in Wiltshire is 1-2 km in width and the study area 34.8 km in length. In addition to the river valley, several gravel pits were frequented by swans. The Mute Swan population in that area has been studied since 1978 when ringing commenced also (Trump et al. 1994). Between 1978 and 1993 the total population increased due to an increase in the number of non-territorial birds while the number of territorial and breeding pairs remained fairly constant.

Ayrshire

Mute Swans in an area comprising the old county of Ayrshire were studied from 1984 to 1986 by Leach (1988). No ringing was undertaken. The total population was fairly constant during the study period but the number of non-territorial birds and the number of territorial and breeding pairs had decreased substantially between 1955 and 1983.

Orkney

On the Lochs of Harray and Stenness in Orkney a large increase occurred in swan numbers between 1983 and 1990 (Meek 1993). The study area covered 19.3 sq km and consisted of a loch system with a gradation in salinity from virtually sea water in the Loch of Stenness to fresh water in the Loch of Harray. A substantial decrease in the population between 1990 and 1992 was associated with a marked decline in the growth of Canadian Pondweed *Elodea canadensis*. The large number of breeding pairs in 1990 included a number of colonial nesting pairs on the Loch of Harray.

Outer Hebrides

A study of Mute Swans in the Outer Hebrides from 1978 to 1982 included a programme of colour ringing (Spray 1981). The study area, about 210 km in length, comprised the islands of North Uist, South Uist and Benbecula which are situated almost 50 km west of the Scottish mainland. Spray (1991) suggested the population was stable, with low productivity being balanced by high rates of adult survival.

Lothians

The first survey of breeding Mute Swans in the Lothians was organised by C.P. Rawcliffe in 1953/54 (Rawcliffe 1954 and 1955). Since there were no reports of swans on the River Tyne in East Lothian during the survey it was concluded that coverage in the Lothians was incomplete. Rawcliffe counted nesting pairs in Edinburgh in 1955 and 1956 (MacMillan 1958) and A. T. MacMillan undertook a survey of breeding swans in Edinburgh in 1957 and in 1958 (MacMillan 1958). Results suggested there had been an increase in the number of breeding pairs in Edinburgh from 8 in 1953, to 11 in 1958.

Results from the national census in 1961 revealed that the number of breeding pairs in Edinburgh had increased to 15 and the total population in the Lothians numbered 249 birds including 52 breeding pairs (Brown and Brown 1984). I. B. Roy and W. M. Skene (1961) undertook a thorough survey in East Lothian in 1961 and found 24 breeding pairs of which 13 were located on the River Tyne.

Concerns were expressed by local ornithologists in 1976 regarding the apparent decline in the number of Mute Swans in the Lothians and resulted in the population being surveyed in 1977. The survey revealed that only three pairs bred in Edinburgh and twelve pairs in East Lothian, with just six pairs on the River Tyne (Vick 1978). The total population in the Lothians in 1977 was 116-118 birds (Brown and Brown 1984).

The Lothians population was surveyed in 1978 as part of a national census and the numbers of birds recorded in Midlothian, Edinburgh and East Lothian were similar to those for 1977 (Ogilvie 1981).

Although the European Mute Swan population had increased in numbers during the 1970's and early 1980's the British population declined during the 1960's and 1970's numbers increased only during the 1980's, however, there was considerable regional variation. Coarse fishing was not prevalent in Scotland, including the Lothians, thus lead poisoning due to the ingestion of lead fishing weights was not the cause of the population decline in those areas. Many local ornithologists were concerned that the Lothians population might decrease still further in years subsequent to 1978. For that reason, a long-term population monitoring programme was instigated in 1978. By 1980 the number of birds in the total population had shown little change, although the number of breeding pairs had increased.
In 1981 the scope of the study was extended to include collection of data relating to cygnet survival prior to fledging in order to compare productivity in the Lothians with that in other areas of Britain. There was a possibility that poor productivity in the Lothians, due to

environmental factors, had contributed to the population's decline. Colour ringing commenced in 1982 and this enabled the collection of the data required to estimate values for the parameters affecting the dynamics of the breeding population. These parameters included post-fledging survival to breeding age, age specific proportions of swans breeding for the first time, immigration, emigration and mortality in the breeding population (Figure 1). By measuring the parameters as precisely as possible and entering them into a model of the populations dynamics it would be possible to investigate their potential contributions to population change. Additionally, such a model would be appropriate to studies of population dynamics in other species.

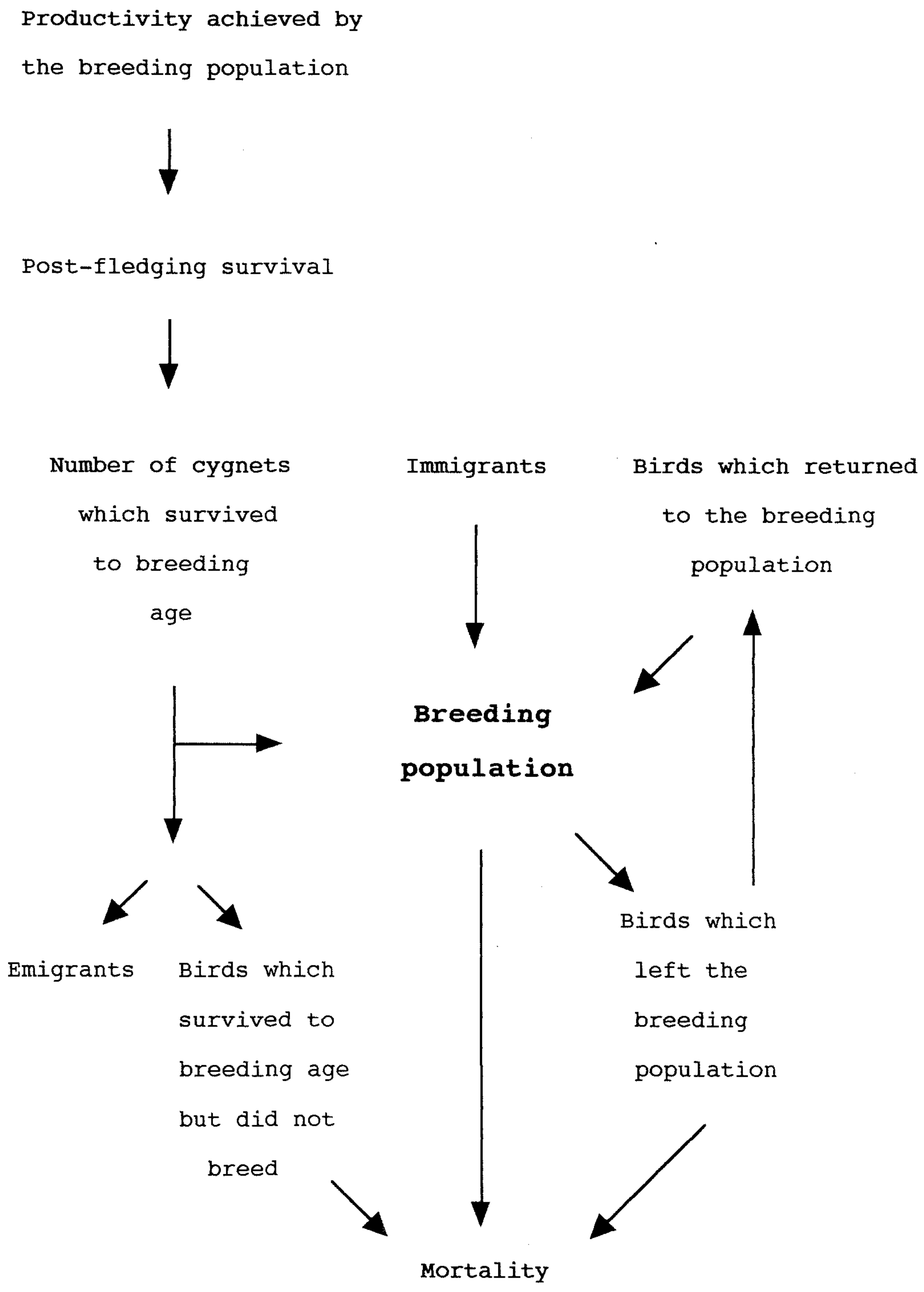


Figure 1. Demographic parameters which effectively controlled the number of pairs of Mute Swans which bred in the Lothians.

Chapter 2

Literature Review

The aim of the study was to determine whether the Mute Swan population in the Lothians had the capacity to sustain its numbers between 1978 and 1993 through its own productivity or whether it was dependent upon immigration. Therefore, this review concentrates on publications arising from studies in which the dynamics of Mute Swan populations were investigated. The number of such studies which produced data comparable to the present study was constrained by the requirements for a substantial proportion of the population under investigation to be colour ringed and for long-term monitoring of marked swans.

Pre-fledging survival

In the Oxford area Reynolds quantified survival among cygnets at 50% over a period of 20 weeks, from April to September in 1964 (Reynolds 1965; Perrins and Reynolds 1967). Bacon (1980), during his study in the Oxford area from 1976 to 1978, found survival in the first 12 weeks after hatching differed little from the findings of Reynolds over the same period. By 1980 there had been no increase in the number of breeding pairs of swans in the area; however, the number of gravel pits had increased. These new water bodies apparently provided a more successful habitat for breeding swans since Birkhead and Perrins (1985) estimated survival between hatching and 20 weeks at 78% during the period 1980 to 1982.

Lead poisoning in the lower Thames area contributed to the low level of pre-fledging survival of 46% to the age of 20 weeks from 1980 to 1982 (Birkhead and Perrins 1985). Pre-fledging survival in the South Staffordshire area was given as 76% during the period 1966 to 1978 (Coleman and Minton 1980) and 73% for the period 1966 to 1985 (Coleman et al. 1991).

In the Cork area of Ireland Smiddy and O'Halloran (1991) found that 76% of cygnets which hatched later fledged and the greatest loss amongst unfledged cygnets occurred early in the breeding season.

Published results indicate that pre-fledging survival of cygnets was generally between 70% and 80%. Perrins (1991a) demonstrated that low survival in the Oxford area in the early years of the study was sufficient, in fact, to maintain the size of the population. He found also that low survival in the Thames area and comparatively high survival in South Staffordshire were insufficient to maintain their respective populations. Pre-fledging survival rates alone, therefore, were not necessarily indicative of a population's ability to be self-sustaining.

Number of cygnets fledged per breeding pair

It was not always possible for swan biologists to count the number of breeding swans in some populations at the commencement of breeding seasons, for example Ulfvens (1993) was only able to visit islands in the archipelago of Ostrobothnia on the west coast of Finland in late May/early June. It was possible that his count of breeding pairs did not include some which failed at an early stage since some clutches had hatched prior to his arrival on the islands. A number of studies reported productivity as, for example, the number of cygnets fledged per successful breeding pair or brood size at fledging. Such measurements of productivity take no account of the number of pairs which failed in their breeding attempt at some stage during the breeding season and consequently they represent productivity from a section of a breeding population only. The difficulties involved in the accurate measurement of the number of cygnets which fledge caused a number of swan biologists to quantify productivity as the number of cygnets per breeding pair raised to a specified number of weeks after hatching.

In the Oxford area Perrins and Reynolds (1967) estimated 2.0 cygnets fledged per breeding pair while Bacon (1980) gave a figure of 2.3 cygnets per breeding pair at 12 weeks. Birkhead and Perrins (1985) found that each breeding pair raised 3.8 cygnets in the Oxford area and 2.1 cygnets in the lower Thames area to the age of 20 weeks.

Productivity in South Staffordshire between 1960 and 1967 ranged from 1.7 to 2.3 cygnets fledged per breeding pair with a mean of 2.0 (Minton 1968). Coleman and Minton (1980) gave only the brood size at fledging for the period 1966 to 1978. Coleman et al.(1991) found productivity was lower in the industrial area than the rural area and gave an overall mean for the period 1966 to 1985 of 2.0 cygnets fledged per breeding pair.

Perrins and Ogilvie (1981) indicated that productivity was quite low at Abbotsbury. Trump et al. (1994) establish productivity at 2.1 cygnets fledged per breeding pair in the Wylye Valley, Wiltshire.

Spray (1981a) determined, from the data of Jenkins et al. (1976), that 1.4 cygnets fledged per breeding pair for the period 1971 to 1974 in the Hebrides and that 1.8 cygnets fledged per breeding pair for the period 1978 to 1982. He also found that productivity was greater on eutrophic lochs than on mesotrophic and saline lochs.

Collins (1991) found that 2.7 cygnets fledged per breeding pair in the Dublin area with a range from 0.6 cygnets fledged per breeding pair on estuary habitat to 3.4 cygnets fledged per breeding pair in urban areas. In the Cork area 3.5 cygnets fledged per pair which built a nest and 3.8 cygnets fledged per pair which laid eggs (Smiddy and O'Halloran 1991).

Bacon and Andersen-Harild (1989) gave a productivity figure in Denmark in 1966 of 3.5 cygnets fledged per solitary breeding pair and 1.9 cygnets fledged per colonial breeding pair. Subsequently, during the 1970's, productivity declined in those areas to 2.5 cygnets fledged per solitary breeding pair and 1.1 cygnets fledged per colonial breeding pair. Egg loss due to trampling by colonial swans accounted for much of the difference in productivity between solitary and colonial pairs (Andersen-Harild 1981).

Esselnk and Beekman (1991) gave only the number of cygnets fledged per successful breeding pair in the Groningen area of the Netherlands for the years 1984 to 1989. The number of breeding pairs and the number of fledged cygnets were presented graphically but not tabulated, so the precise number of cygnets fledged per breeding pair could not be determined.

Scherner (1991) investigated productivity in the Wolfsburg and Göttingen areas of Germany. However, it is considered that the number of pairs breeding per annum were too few (65 breeding attempts in the Wolfsburg area between 1955 and 1986, equivalent to a mean of 2.0 breeding pairs per year; 39 breeding attempts in the Göttingen area between 1972 and 1986, equivalent to a mean of 2.4 breeding pairs per year) to produce meaningful productivity values. Only 89 cygnets fledged in the Wolfsburg area between 1966 and 1975 (Latzel and Scherner 1985).

It was apparent that considerable variation occurred in productivity rates between areas and that in some cases these rates changed within areas over a period of time. The figure of 2.1 cygnets fledged per breeding pair in the lower Thames area was insufficient to sustain that population (Birkhead and Perrins 1985) and yet 2.1 cygnets fledged per breeding pair in the Wylye Valley and 1.8 cygnets fledged per breeding pair in the Hebrides were considered sufficient to maintain their respective populations (Trump et al. 1994; Birkhead and Perrins 1986). Consequently, this parameter cannot be used in isolation to infer population trends.

Post-fledging survival

Survival was investigated in the Oxford area between 1960 and 1966. Survival rates were calculated for the first four years after fledging; first year survival was 67.9% (Perrins and Reynolds 1967). Data were rather few for the fourth year due to the relatively short period of the study and additionally there were periods of particularly cold weather during the winters 1961-1962 and 1962-1963 when mortality amongst swans in Britain was exceptionally high (Boyd and Ogilvie 1964). Consequently survival rates from the Oxford area for the period 1960 to 1966 were abnormally low (Perrins and Reynolds 1967).

Bacon (1980) also estimated post-fledging survival in the Oxford area, however his data were few and the study period too short to obtain accurate survival rates. Post-fledging survival was not investigated by Birkhead and Perrins (1985) and in their life table they utilised the rather out-dated and abnormally low post-fledging survival rates from Perrins and Reynolds (1967). Data in Perrins and Reynolds (1967) and Bacon (1980) were utilised also in the construction of life tables by Birkhead and Perrins (1986). More recent post-fledging survival rates for the Oxford area were utilised by Bacon and Perrins (1991) and by Perrins (1991a) in balancing productivity against mortality in breeding populations.
First year post-fledging survival was particularly low during the early 1980's with rates of 36% in the Oxford area and 38% in the lower Thames area (Perrins 1991a). The cause of this high mortality was lead poisoning (Sears 1986).

The long-term nature of the study in the Wylye Valley enabled estimates to be made for up to the fifth year post-fledging based on 499 birds ringed as cygnets from 1974 to

1987 (Trump et al. 1994). Survival in the first year was 63%.

Birkhead and Perrins (1986) gave survival rates in the Hebrides for the first four years post-fledging, although they were based on a small number of observations. Their figure for the first year was 58%. Spray (1991) reported a first year survival rate of 42% but gave no estimate for years two, three or four.

Survival rates up to five years post-fledging from the long-term study at Abbotsbury were based on a large number of observations. First year survival varied from 38% to 92% with a mean of 68% during the years 1970 to 1979 (Perrins and Ogilvie 1981). Birkhead and Perrins (1986) suggested the mean was about 70%. Survival rates for the Abbotsbury area were not updated nor the number of age classes extended in Perrins et al. (1994).

Coleman and Minton (1980) presented survival rates for the first five years post-fledging from the period 1961 to 1977 in South Staffordshire. They found survival in the first year was just 41.4%. Coleman et al. (1991) found mortality was greatest in the first year (43.4%) and gave figures for the first five years for the period up to 1985.

Andersen-Harild (1981) found survival amongst first year birds hatched by solitary breeding pairs was 44% and that survival amongst first year birds hatched by colonially breeding pairs was 36%. Swans hatched in colonies tended to be lighter in weight at fledging than birds hatched by solitary breeding pairs and this factor contributed to the difference in survival rates. Survival was greater in older birds but varied with the severity of winter weather. Bacon and Andersen-Harild (1989) published survival rates for the first six years post-fledging and indicated the inter annual variation during the first year was 30% to 86%.

Survival rates from two areas of Germany were presented by Scherner (1991). His calculations were based on survival to the age of seventeen years of 102 birds ringed in the Wolfsburg area and on survival to the age of thirteen years of 26 birds ringed in the Göttingen area. Since the number of birds alive at the start of each age class was relatively few these findings must be treated with some caution. Survival in the Wolfsburg area was higher during the first year after fledging than in most British study areas. In the Göttingen area the figure was even higher and, in contrast to survival rates in many areas of Britain, it was higher than in most of the subsequent twelve years.

Ogilvie (1967) analysed ringing data for Britain held by the British Trust for Ornithology (B.T.O.) for the period 1959 to 1965 and calculated survival rates for the first four years from 1st July prior to fledging. He found a 60% survival rate in the first year and also that survival in the second, third and fourth years did not exceed 68%. Perrins (1991b) analysed the ringing and recovery data for Mute Swans held by the B.T.O. up to 1988. Survival rates were calculated for the first seven years post-fledging. Survival was found to be lowest in the first year and to increase in each of the following three years to peak in the fourth year after which there was a small decrease in each subsequent year. Seasonal changes were also reported which indicated that mortality was not constant throughout the year. Since survival rates were presented graphically, not tabulated, it was not possible to extract precise estimates from the paper but first year survival appeared to be about 55%.

From the ringing and recovery data held by the B.T.O. the principal cause of death amongst Mute Swans in Britain was identified as flying accidents (Perrins and Sears 1991). A similar conclusion was reached by Brown et al. (1992) from the results of post-mortem examinations of 366 British swans between 1951 and 1989.

Although a number of Mute Swan studies commenced in the early 1960's no estimates of survival rates beyond the age of six years have been published. Some novel but rather irrelevant information has been published, for example the age of the oldest wild Mute Swan recorded in Britain was 26 years (Bacon and Andersen-Harild 1989), yet no details have been presented regarding the life span of the majority of birds in the country.

Birkhead and Perrins (1986) indicated the average expectation of further life for adult swans on the Thames was about 5 years, in the Hebrides 9.5 years and at Abbotsbury 16 years. These calculations were based, however, on the assumption that survival was constant through adult life. Since that assumption has not been established the figures should be treated with caution. Indeed, Perrins (1991b) has shown that survival is not constant and a decline in survival in the terminal years of life may occur. A terminal decline has been established in a number of other species (Newton 1989b). Since a number of studies have continued for over thirty years it is unfortunate that greater attention has not been given to long-term survival in Mute Swan populations.

Mortality in the breeding population

Perrins and Reynolds (1967) estimated, from the loss of ringed breeding swans from their study area, that 18.1% of breeding birds died each year in the Oxford area during the period 1960 to 1966. They found mortality in the breeding population did not increase as a result of the cold winters of 1961-62 and 1962-63. A mortality figure of 20% was determined by Bacon (1980) for the period 1976 to 1979. Birkhead and Perrins (1985) determined that mortality was 15.1% for the period 1979 to 1982 in the Oxford area and 34% in the lower Thames area where it was high due to lead poisoning.

In the Wylye Valley mortality was estimated, for the period 1978 to 1990, at 12.9% per annum (Trump et al. 1994). The estimate for the Hebrides was 10% (Birkhead and Perrins 1986).

Up to 1979, mortality was 6.4% at Abbotsbury and 13.8% at Radipole (Perrins and Ogilvie 1981). Perrins et al. (1994) gave figures for male (22.1%) and female (19.5%) mortality for the period 1977 to 1991, and reported a wide range (from less than 10% up to 50% per annum) for both sexes.

Minton (1968) found that 20% of breeding birds died each year in South Staffordshire from 1961 to 1967 and, in contrast to findings from the Oxford area, that mortality was particularly high during the year 1962 to 1963 due to severe winter weather. Mortality during the period 1961 to 1985 was 21% per annum (Coleman et al. 1991). Andersen-Harild (1981) found little difference in mortality between solitary and colonial breeding birds during his study in Denmark; mortality amongst solitary breeding pairs was 19.4% per annum.

Mortality in breeding populations was generally around 20%. The particularly high rate of survival in the Hebrides may have resulted from fewer collisions due, for example, to a lower density of obstacles such as high pylons and buildings than in other study areas in Britain.

Age at first breeding

The age at first breeding ranged, in the Oxford area, from 2 years to 6 years for females and 3 years to 6 years for males with an average at 4 years (Perrins and Reynolds 1967). However, these findings were restricted by the relatively short length of the study.

Trump et al. (1994) found that the mean age in the Wylye Valley was 4.5 years, although no range was given.

At Radipole a mean age at first breeding was not estimated by Perrins and Ogilvie (1981), but the range was given as 3 to 10 years; no values were presented for Abbotsbury. They suggested females bred for the first time at an earlier age than males, however, this was based on the 1976 cohort only. Perrins et al.(1994) found the range at Abbotsbury to be 2 to 9 years for both sexes although no mean was given.

In South Staffordshire, between 1960 and 1967, a mean of 3.8 years with a range of 3 to 6 years was established for males and 3.6 years with a range of 2 to 6 years was established for females (Minton 1968). The study by Minton (1968) appeared to be the only one in which age specific proportions of swans which bred for the first time were quantified. However, results from this study must have been truncated by its relatively short time scale.

Coleman and Minton (1979) did not present the proportion of birds which progressed to breed in each age class; instead they gave the proportions of paired birds which progressed to breed in each age class. This point appeared to have been overlooked by Birkhead and Perrins (1986) in their table listing the age at which birds commenced breeding in different study areas. Although it was possible to determine the age at which birds paired for the first time in the sedentary South Staffordshire population it was not possible to do so in mobile populations where pairs may have been established outside the study area and gone unrecorded.

Coleman and Minton (1979) found the proportion of paired two year old swans which progressed to breed was lower in the early years of the study than in more recent years and suggested that the age at first breeding might have reduced. However, the mean age at which birds bred for the first time and the age range of such birds were not specified. From the available information it was difficult to determine a change in the age at which birds bred for the first time.

The age at first breeding in the Hebrides was not investigated due to the relatively short period of the

study. However, no 2 or 3 year old birds bred for the first time and only one bird from a possible 25 (4%) which reached the age of 4 years actually bred (Birkhead and Perrins 1986). The actual mean would probably be greater than in many British populations studied to-date.
The age of first breeding in the Dublin area ranged from 2 to 6 years (Collins 1991) but the data were too few and the study period too short for these findings to be meaningful.

The estimate of five years for solitary breeding birds given by Andersen-Harild (1981) was constrained by the small number of years for which data were available from the Danish study at that time. He found that, as was the case in the Hebrides, no third year birds had bred and less than 10% of birds in their fourth calendar year bred. No data were available for colonial breeding birds. Bacon and Andersen-Harild (1989) found fewer than 1% of birds bred for the first time by the age of 3 years, that the age range was 2 to 15 years for females and 2 to 11 years for males. The overall mean, the mean for females and the mean for males were each 5.7 years.

In order to construct an accurate life table it is necessary to determine the range of ages at which Mute Swans breed for the first time and to quantify the proportion of birds which breed for the first time in each age class. The latter parameter has clearly been ignored in many studies. This has led to the use of the mean age at first breeding in conjunction with the assumptions that all birds which survive to the mean age of first breeding actually breed and that emigration, from study areas, does not occur (Birkhead and Perrins 1986; Bacon and Perrins

1991).

Perrins and Reynolds (1967) noted the presence, in a non-breeding flock, of a bird aged seven years which had apparently never bred and Andersen-Harild (1981) indicated that some birds probably never breed. Since it was probable that a number of swans in each study area never breed then the assumption that all birds which survive to the mean age of first breeding actually breed was not a satisfactory procedure in the construction of life tables for Mute Swan populations.

Immigration and Emigration

Atkinson-Willes (1981) divided the population in the British Isles into four groups-

1. England and Wales
2. Scotland; mainland and Orkney
3. Scotland; Hebrides
4. Ireland.

These groups were devised from ringing data and results from population studies. Up to that time (the paper was presented at the Second International Swan Symposium held in Japan, February 1980) long-term studies, for which data would have been available, were being conducted at Abbotsbury in Dorset, Oxford, South Midlands and Stratford-on-Avon in Warwickshire. The majority of swans in those areas were found to move only short distances up and down water courses and it was presumed that Mute Swans throughout Britain conformed to such behaviour (Ogilvie 1967). Consequently the B.T.O. ringing department was reluctant to accept reports, at least up to 1981, of Mute

Swan ring sightings from birds found to have moved a substantial distance within Britain; it was suggested that the digits on the rings of such swans had been mis-read (B.T.O. pers comm.). It was inevitable, therefore, that very few swans from studies in the southern half of England would have been recorded in Scotland or Ireland.

Perrins (1991b) listed the number of swans ringed by region up to 1975. Of the 26,468 ringed, 140 (0.5%) had been ringed in Ireland and 921 (3.5%) in Scotland, including a single swan in the Hebrides. He estimated that 26.5% of swans ringed in Britain were recovered dead. Since relatively few swans were ringed in Ireland or Scotland then very few from there were ever likely to be found elsewhere.

There was, therefore, little evidence to justify the separation of the Hebrides population from the rest of Scotland especially as populations on all other islands, including the Orkney Islands, were grouped with mainland Scotland. Indeed Jenkins et al. (1976) concluded from their study of the Hebrides population from 1971 to 1974 that up to 200 immigrants moulted on the islands each July.

Spray (1981a) demonstrated that an influx of swans did not, in fact, occur in the Hebrides in July and that the apparent increase in the number of swans at that time was due to an error in the censusing technique employed by Jenkins et al. However, amongst the birds ringed on the Hebrides between 1978 and 1982, 14 were found on the north coast of Ireland (Smiddy and O'Halloran 1991), 1 in Shetland (Spencer and Hudson 1982), 1 at Stranraer (Mead and Hudson 1983) and 1 on the Island of Gigha (Mead and Hudson 1986). Spray (1981b) noted that 4 birds had been reported from Lewis and Harris, 2 from Skye and 8 from Tiree and indicated that a number might also be expected to reach the Isle of Man. He suggested that the actual number of swans moving from the Hebrides to Ireland might greatly exceed the number reported. There were no records of those ringed birds having returned to the Hebrides (Spray pers. comm.).

No population in Scotland can be described as closed nor independent of those in England and Wales. Indeed in recent years a number of movements between Scotland and England have appeared in the annual ringing reports.

The B.T.O. no longer has the administrative capacity to routinely accept records of live Mute Swans which move less than 40 km. As a result relatively few movements between adjoining counties or regions in Scotland have been entered in the national ringing scheme in recent years. That lack of records appeared to cause Kirby et al. (1994) to erroneously assume that virtually no movements occurred at a local level. Collins and Wheelan (1993 and 1994) demonstrated that Mute Swans in Ireland can move considerable distances, thus that population cannot be described as sedentary either.

In recent years, three of Atkinson-Willes' British sub-groups were combined to form one British sub-group while the Irish population remained separate (Monval and Pirot 1989). However, the presumption that the entire population in Britain is virtually sedentary still persists in some quarters (Kirby et al. 1994) as does the presumption that the Hebrides population is isolated (Spray 1991; Gibbons et al. 1993).

Immigration and emigration have been disregarded in life tables relating to swan populations in Britain due to the assumption that Mute swans rarely moved far (Birkhead and Perrins 1986; Perrins 1991a).

Perrins and Reynolds (1967) noted that some birds did leave the Oxford study area, but they did not estimate the number involved. Bacon (1980) mentioned the presence of immigrants in the Oxford area, some of which bred, but their numbers were not quantified.

Perrins and Ogilvie (1981) noted movements between Abbotsbury and Radipole and the Exe estuary 56 km distant, and between Abbotsbury and Radipole and Poole and Chichester some 40-60 km distant. They estimated that 25% of birds in the breeding population at Abbotsbury were immigrants; emigration was not quantified. No estimate was given for immigration in more recent years, however, Perrins et al. (1994) indicated that due to a change in the management technique at Abbotsbury, the number of immigrants in the breeding population had decreased in recent years.

A number of emigrants were recorded in the South Staffordshire area by Coleman et al. (1991) and they determined that 5% of breeding population were immigrants during the period 1966 to 1985.

Trump et al. (1994) indicated immigration to the breeding population had occurred but the origins of such birds were unknown. They also noted movements to and from the Avon Valley and it must be concluded that some birds emigrated from the Wylye Valley and bred elsewhere.

Meek (1993) indicated that up to 400 birds left the Orkney Islands during 1991; since they were unringed their destinations were unknown and some may have survived to breed outside the Orkney Islands.

Each of the above studies reported the occurrence of immigration and emigration with estimates for the former varying from 5% to 25%. Even though estimates may be low in a specific population, their impact on the dynamics of that breeding population may be considerable and, therefore, the parameters should be included in any assessment of a population's ability to sustain its numbers.

Number of breeding birds which left the breeding population and the number of such birds which returned to the breeding population.

Estimates of birds leaving the breeding population were 18.7% per annum at Abbotsbury and 24.9% per annum at Radipole (Perrins and Ogilvie 1981). The proportion of these birds which subsequently returned was not stated.

Andersen-Harild (1981) found 10-20% of surviving breeding birds did not breed in any one year in his Danish study. The figure rose to 42% after the very severe winter of 1970.

The debit effect on a breeding population of this parameter was also identified by Bart et al. (1991).

Life table

Life tables have been constructed for a number of Mute Swan populations in which productivity is balanced against loss

through mortality.
Perrins and Reynolds (1967) suggested there was an equal balance in the Oxford population during the period 1960 to 1966, although they acknowledged that the number of data were too few to form a firm conclusion. It should be noted that they used a mean age of first breeding and that the age specific proportions of first breeders, immigrants and emigrants were not included in their table.
Bacon (1980) found productivity exceeded mortality in the Oxford breeding population during the period 1976 to 1978 and concluded that the excess cygnets dispersed out of the study area. Around 20% of cygnets hatched in the study area were later recorded outside it but may have returned at a later date. He utilised also a mean age at first breeding. Age specific proportions of first breeders, immigrants and emigrants were not included.
Birkhead and Perrins (1985) based their life table on mean age at first breeding and post-fledging survival rates from Perrins and Reynolds (1967). They found productivity exceeded mortality in the Oxford area but not in the lower Thames. Age specific proportions of first breeders, immigrants and emigrants were not included in their calculations.

Trump et al. (1994) found productivity exceeded mortality in the Wylye Valley. They also assumed a mean age at first breeding while the age specific proportions of first breeders, immigrants and emigrants were not incorporated in their life table.

Andersen-Harild (1981) calculated that sufficient young were produced from solitary pairs to account for a 15%

increase in the population in his study area. In addition he found that productivity from the colonial population was so poor that that population should have declined in numbers. In fact, the colonial population increased in numbers due to immigration.

Discussion

A number of species, for example the Puffin *Fratercula arctica* (Harris and Wanless 1991), the Gannet *Sula bassana* (Nelson 1978) and the Sparrowhawk *Accipiter nisus* (Newton 1986), have been intensively studied over a long period of time. Measurements of demographic parameters through ringing enabled investigations to take place into the ability of those species in different areas to sustain their numbers through their own productivity and the extent of their dependence on immigration to increase the size of their populations.

Although a number of studies into Mute Swan populations commenced over thirty years ago it is clear from the available publications that many demographic parameters have yet to be thoroughly investigated. Given that measurements of some parameters were based on insufficient data to give reliable results, it is apparent that an understanding of the dynamics of Mute Swan populations is far from complete.

Chapter 3

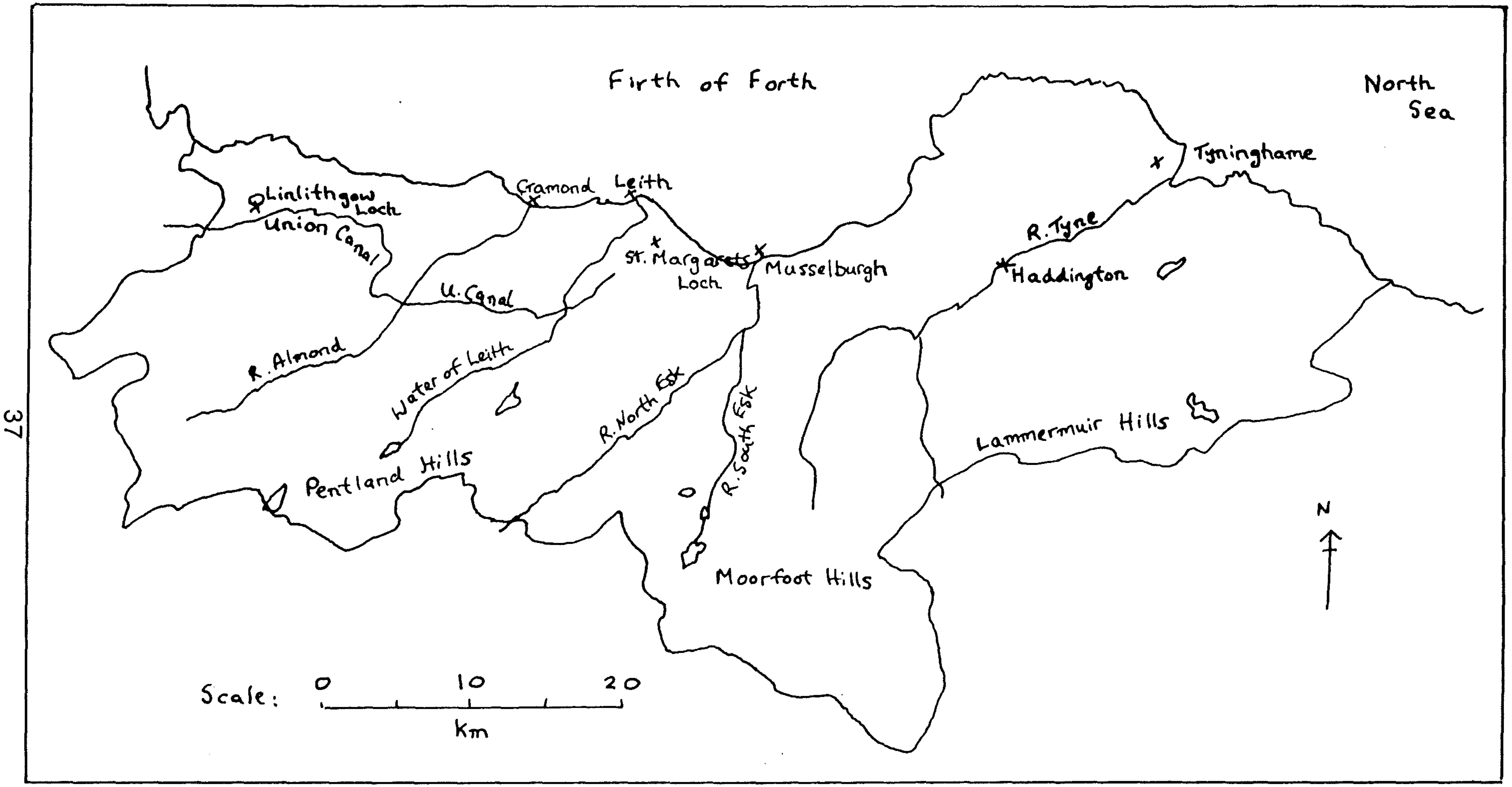
Study Area and Methods

Study Area

The study area comprised the old counties of West Lothian, Midlothian and East Lothian in addition to the City of Edinburgh. It was similar to but not identical with the recently devolved administrative area of Lothian Region. In order to facilitate direct comparison of population counts from earlier years with those collected during the present study, and to avoid complications which might arise as a result of future boundary changes, the old county system was chosen as the boundary for the present study.

The Lothians study area covered 2,000 sq km. It was bounded in the north by the Firth of Forth, to the east by the North Sea and to the south by the Lammermuir, Moorfoot and Pentland Hills which reached a height of 535m above sea level. There were no geographical boundaries to the west where the study area merged into the central belt of Scotland. Principal water-bodies and water-ways are illustrated in Figure 2.

Figure 1 Lothians Study Area



Methods

Background

It was apparent from The Atlas of Breeding Birds in Britain and Ireland (Sharrock 1976) and The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991 (Gibbons et al. 1993) that Mute Swans bred widely in the Lothians. The winter distribution of the species, depicted in The Atlas of Wintering Birds in Britain and Ireland (Lack 1986), closely resembled the summer distribution. For the purpose of the present study, it was anticipated that Mute Swans would be located on or in the vicinity of still waters and main river systems throughout the study area, in addition to the Union Canal in West Lothian and in Edinburgh.

A list of sites frequented by Mute Swans in earlier years was compiled from a number of sources and produced valuable background and historical information:-

- Amateur ornithologists' personal field records, many dating back to the mid-1930's.
- Edinburgh Bird Bulletins 1950-1958 (Scottish Ornithologists' Club, Edinburgh).
- Scottish Ornithologists' Club local recorders' annual bird reports for Midlothian and West Lothian (Smith 1968 to 1980).
- A report on Mute Swans in East Lothian in 1961 by Roy and Skene (1961).
- Results from national censuses held in the years 1955-56 (Rawcliffe 1958) and 1961 (Eltringham 1963), and the original data from these censuses.

Ordnance Survey maps covering the study area at 1:50,000 and 1:25,000 scales were systematically searched for additional waters which could have held swans. The resulting list was up-dated following the creation of new farm ponds or loss of sites due to drainage schemes.

In spring Mute Swans could be classed as either non-territorial or territorial. Non-territorial birds tended to collect in flocks while territorial birds were paired, and occupied and defended a territory for their exclusive use. Sites on the list were visited each year in order to quantify the number of birds in each category. Appendix 1 is a copy of the form designed for recording the number of non-territorial swans and Appendix 2 is a copy of the form designed to collate data from each breeding territory. The forms were distributed to ornithologists who had expressed a willingness to assist with the collection of data for the study.

Census techniques

Non-territorial Swans

Non-territorial swans were counted in early and late April from 1978 to 1984. Subsequently this was reduced to one mid-April count once swan numbers in the study area were found to be stable during that month. A group of swan counters was organised annually to undertake a co-ordinated count on a mid-April weekend. Most birds were located in flocks although some single birds were recorded. A few birds may have been over-looked but any under counting was probably balanced by double counting of birds moving between sites. While collating the counts it became apparent that on a few occasions one or two flocks were counted both a.m. and p.m. on the same day and by different counters. Such counts indicated there had been little change in the size of each flock.

Monthly peak counts were also compiled each year from personal field work and local ornithologists' records in order to determine the annual pattern of use of particular flock sites and to identify sites of particular importance in spring.

Territorial Swans

Visits were made to all potential territorial sites between late March and early May from 1978 to 1993 in order to record the number of territorial pairs. All potential territories on the list were visited most years and it was considered that virtually all occupied territories were located annually.

Breeding Swans

Occupied territories were further monitored to determine the number of territorial pairs which progressed to breed. Between 1981 and 1993 regular visits were made to all nesting pairs in the study area throughout each breeding season to enable the recording of the number of breeding pairs which produced cygnets.

Egg laying usually takes place between late March and early May (Birkhead and Perrins 1986) and eggs are laid at about 48hr intervals (Perrins and Reynolds 1967). Only one clutch is laid in a season though a replacement clutch my be laid after early loss of the original clutch. The normal incubation period for Mute Swans is 36 days (Owen and Black 1990) and cygnets take 120 to 150 days to fledge (Birkhead and Perrins 1986). Coleman and Minton (1979) defined a breeding pair in their study as a pair which nested and laid eggs and a non-breeding pair as holding territory, or holding territory and building a nest but not laying eggs. It was not possible, due to the large amount of time which would have been required, to monitor all nests daily at the egg laying stage in the Lothians in order to ascertain whether or not egg laying had commenced. Nests monitored less frequently and found to be empty might have been predated shortly after eggs had been laid (Reynolds 1965; Perrins and Ogilvie 1981) and the nests' proprietors thus incorrectly defined as a non-breeding pair if the Coleman and Minton criteria were applied. Additionally, it was not possible to check all nests for eggs due to access difficulties e.g. nests on islands. In this study, therefore, breeding pairs of swans were defined as paired birds which defended a territory for a period of time sufficient to construct a substantial nest.

Collection of precise data on full clutch size and the actual number of cygnets hatched per breeding pair were known to be particularly difficult and time-consuming (Bacon 1980; Perrins and Ogilvie 1981; Bacon and Andersen-Harild 1989) and were not attempted. For the same reasons replacement clutches were not routinely identified.

Cygnets

Most breeding swans in the study area hatched cygnets by late May although a few clutches were recorded hatching in June and July. The majority of cygnets fledged by early September, although this ranged from early August to early October. In this study pre-fledged cygnets were categorised as they developed and according to their size as -

small	downy, up to about 3 weeks old
medium	longer-bodied, some evidence of primary and secondary wing feather development
large	primaries and secondaries well developed, not capable of flight
fledged	capable of flight.

Visits were timed in order to record the number of small, medium, large and fledged cygnets each breeding pair raised. Occasionally broods temporarily disappeared, probably into reed beds, adjoining fields or drainage ditches and consequently the number of cygnets in some broods at certain growth stages went unrecorded. In some such instances it was possible to interpolate brood size from subsequent sightings.

Ringing

Observation of broods during the early stages of this study suggested that while many cygnets remained with their parents in the vicinity of their natal site for some time after fledging many other cygnets became independent. These independent birds frequently vacated the natal site and often separated from parents and siblings. At that stage they could no longer be individually identified with regard to natal site and could not reliably be aged after their second winter (Perrins and Reynolds 1967; Minton 1968). Ringing of cygnets prior to these movements, that is prior to fledging, enabled documentation of each ringed cygnet's natal site, year of hatching and identification throughout its lifetime.

During August and September each year from 1982 to 1993 cygnets and their parents were caught and ringed in their breeding territory. Some families vacated their breeding territory during the summer and were caught elsewhere. However, since the movements of these more mobile families were monitored through the summer, and in many instances the parents were already ringed and their breeding site recorded in spring, the natal territory of these cygnets could be documented.

In most instances, permission was obtained from landowners to catch and ring swans on their property. Swans were enticed close enough to hand held bread to be caught, cornered or surrounded by a group of swan catchers, or chased and overhauled by canoeists (Figures 3 and 4). Once caught they were immobilised by tying the legs and wings with strips of cotton fabric (Figure 5). Ringing was undertaken by qualified ringers. An individually numbered British Trust for Ornithology metal ring (Incoloy, size M) (Figure 6) was fitted, with the aid of large ringing pliers (Figure 7), on one leg. A coloured Darvic (laminated PVC) ring inscribed with a unique combination of three numbers or letters (Figure 6) was fitted on the other leg. The overlap on the Darvic ring was secured with a quick setting, water-proof Marley Solvent Cement KS2. Sellotape was wound round the ring in order to temporarily hold the shape of the ring until the cement had bonded with the Darvic. This allowed swans to be released more rapidly than would have been the case if they were released after the cement had hardened.

Ring digits could be read at a considerable distance and subsequent movements of ringed individuals could be monitored without the need to retrap (Ogilvie 1972b). White Darvic rings were used during the present study but, as the digit combinations had diminished by 1993 and it was proposed to continue ringing for a number of years, green Darvic was introduced in 1995.

The colour and digit combinations varied between study areas, for example blue and red were used in Northumberland and orange in Argyll (Figure 6) while yellow was used at Abbotsbury and also in some Whooper *Cygnus cygnus* and Bewick's *Cygnus bewickii* swan studies. The allocation of colour and digit combinations to swan biologists and coordination of sighting records was undertaken in Britain by the Wildfowl and Wetlands Trust, Slimbridge.

Figure 3. Canoeists preparing to catch swans

Figure 4. Canoeist delivering cygnets to the ringing party

Figure 5. Mute swans ready to be ringed

Figure 6. Incoloy and Darvic rings

Figure 7. Ringing equipment

Where an adult was already ringed the rings were inspected for wear and damage and replaced if necessary. Rees et al. (1990) found that some Whooper and Bewick's swans broke or lost their Darvic rings more frequently than others. This was also the case with Mute Swans in the present study, therefore, considerable effort was directed at detecting and retrapping any bird which carried a damaged ring or had lost a ring. There was a greater tendency for damage or loss to occur to Darvic rings rather than metal rings. A bird which lost one ring was still identifiable from its remaining ring number. During the period 1982 to 1993 a total of 1098 individual swans were ringed in the study area and of these 0.46% (4 males and 1 female) were later retrapped in order to replace a lost metal ring. These individual birds remained identifiable by their Darvic code. Consequently the number of birds which lost both rings, and were therefore unidentifiable, was too few to affect data analyses.

Determination of sex

Sex was determined by cloacal examination following the procedure of Hochbaum (1942) and Hanson (1967) and applied to Mute Swans by Bacon and Coleman (1986). The sex of cygnets and adults was determined at the time they were captured for ringing.

Owen (1982) described the accuracy of cloacal examination in Barnacle Geese as not biased according to age; however, Bacon and Andersen-Harild (1989) described the accuracy as reliable for adult Mute Swans, but less so for cygnets. Carl Mitchel (pers.comm.) indicated that from his experience of sexing Canada Geese by cloacal examination an error of 5-10% would be expected. The technique did, therefore, appear to be susceptible to inaccuracy. Although cloacal examination was widely practised on Mute Swans, the level of accuracy achieved in those studies was invariably not addressed and the technique was assumed to be accurate.

Bacon and Coleman (1986) determined that cygnets of different sexes had different growth rates and suggested that skull growth might take precedence over feather growth if the food supply was inadequate for a normal rate of growth. Mathiasson (1981b) showed that skull growth was almost complete at the age of fledging. Thus, the skull of a male could generally be expected to be larger than that for a female with the difference well defined just prior to fledging. Mathiasson (1981b) found that, at hatching, female cygnets were lighter than males and that the differential increased with time resulting in males being 28% heavier at fledging. He also found, as might be anticipated in nidifugous young, that tarsus growth commenced early and levelled out comparatively early and that tarsii were generally larger in males than females. In the Lothians, the age of cygnets varied at the time of ringing and a considerable range of values for each biometric parameter was therefore anticipated for both males and females. Swans tended to defaecate between capture and release, possibly two or three times, and such variable weight loss required to be taken into account when determining sex. Comparison of biometric data <u>within</u> broods did, however, appear to offer an alternative to cloacal examination as an approach to determining the sex of cygnets which were large enough to be ringed. The weight, tarsus length and skull length of cygnets recorded at the time of ringing were utilised for this purpose. Weight was measured on a Pesola spring balance with a capacity of 20kg (Figure 7). Skull and tarsus lengths were measured using dial reading plastic callipers (Figure 7).

Given that males were generally larger than females it was possible to determine the sex of each cygnet within a brood from their biometric data. Where all cygnets had similar measurements and differentiation was unclear then measurements from the parents were helpful for comparison, particularly when the cygnets were close to fledging and growth of the tarsus of each cygnet was almost complete. If the majority of cygnets in a brood weighed less than 5.5 kg, it was frequently impossible to separate males from females due to the lack of differential in growth rate between the sexes.

The sex of breeding adults was determined from their behaviour during the breeding season and by comparative size within pairs or from biometric data if caught.

The accuracy of each method was investigated by comparing the sex of ringed adults with their classification at the time of ringing.

Monitoring the movements and survival of ringed swans

Regular observations were made of swans which frequented the study area and their ring numbers recorded. Ring numbers of territorial or breeding birds were recorded in addition to year round recording of ring numbers of birds in flocks. Monitoring outside the study area was less intense and birds which permanently moved away from the

Lothians may have been overlooked. However, ringers of swans frequently exchanged information regarding sightings of ringed immigrants in their study area, for example in Northumberland, Borders, Strathclyde, Argyll, Fife, Tayside and Grampian. In addition, requests for details of sightings of ringed Mute Swans were periodically placed in ornithological publications and generated additional information from ornithologists and members of the public. The British Trust for Ornithology provided a list of all their ringing recoveries of Mute Swans, up to April 1994. The list comprised all ringed birds found dead or recorded alive in the Lothians and birds ringed in the Lothians but found dead or recorded alive elsewhere. The S.S.P.C.A. Injured Bird Centre at Middlebank, Fife also advised of ringed swans in care or destroyed.

In this study a ringed swan was considered to have died if it had not been sighted during a continuous period of three years (two years for the 1992 cohort, the 1993 cohort was excluded from cygnet survival analyses). Such birds were considered to have died shortly after their last sighting record except in instances where a corpse was recovered and a more precise date of death could be established. A similar procedure was adopted by Owen (1982) during his study of Svalbard Barnacle Geese *Branta leucopsis*. The limitations of this procedure are accepted as resulting in maximum mortality and minimum survival rates (Perrins and Reynolds 1967; Coleman and Minton 1980; Perrins and Ogilvie 1981).

Age

The age of a swan originally ringed as a cygnet in the study area could be determined by reference to original ringing records. A few swans which bred in the study area were ringed as cygnets outside the study area and their ages were determined from B.T.O. ringing records.

The age of swans was determined according to the following criteria:-

- Up to 31st March in the year following hatching a bird was in its first year of life.
- A bird which survived to 1st April in the year following hatching was aged one year, or in its second year of life.
- A bird which survived to 1st April in the following year was aged two years, or in its third year of life.

There was a lack of consistency amongst biologists in categorising the age of Mute Swans. The classification utilised by Perrins and Reynolds (1967), in which a bird was in its first year up to 31st March in the year following hatching and in its second year from the 1st April in the year after hatching to the following 31st March and so on, was comparable to that used in the present study. Perrins and Ogilvie (1981) categorised birds which survived to the September in the year after hatching as first year birds and similarly Coleman and Minton (1980) and Coleman et al. (1991) categorised birds which survived to the August in the year after hatching as first year birds. A swan which survived to the April two years after the year of hatching was aged two years or in its third year of life according to the present study and Perrins and

Reynolds (1967) but was aged just one year or in its second year according to Perrins and Ogilvie (1981), Coleman and Minton (1980) and Coleman et al. (1991). This inconsistency should be borne in mind when comparing results from these different studies, in particular the age at first breeding and age group survival rates.

The March/April cut off date adopted in the present study coincided with the beginning of each new breeding season.

Altitude and habitat classification of territories holding breeding pairs

The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991 (Gibbons et al. 1993) described the Mute Swan as rarely occurring above the altitude of 300m. In north-east Scotland in 1978, Spray (1983) found 90% of territorial pairs below the altitude of 90m although large parts of the study area were above the altitude of 100m.

The altitude of each nest site in the Lothians was determined from Ordnance Survey maps with scales 1:50,000 or 1:25,000, in order to investigate the possibility of altitudinal effects on breeding success. The distance between the breeding territory and natal territory of ringed breeding swans was measured on an Ordnance Survey map, scale 1:50,000.

Natal and breeding site habitats were classified, as still water (ponds, lochs and reservoirs), river or canal.

Chapter 4

The Spring Population

Introduction

Mute swan populations in spring comprise non-territorial and territorial birds (Ogilvie 1981). Non-territorial swans tend to collect in flocks which consist primarily of young and sexually immature birds, that is one or two years of age (Birkhead and Perrins 1986). Older swans which had bred in previous years but had lost their mate due to death, injury or divorce and had not re-paired also join non-territorial flocks (Minton 1971). Such flocks were considered to act as a pool of birds with the potential to pair and breed in subsequent springs (Birkhead and Perrins 1986; Coleman et al. 1991; Perrins et al. 1994).

The majority of paired swans which establish a territory during a breeding season have generally done so by April (Ogilvie 1986). Pairs which remain in their territory throughout the previous winter have by March evicted most young remaining from the previous breeding season (Cramp and Simmons 1977). Of the birds which vacate their territories over the winter, due to a lack of food or icing up of waters, those which survive normally return to re-establish their presence at the site by mid-March (Scott 1984).

Not all territorial pairs progress to breed; non-breeding territorial pairs may have been recently paired birds gaining experience in territory acquisition (Minton 1968), which may include spending more time in territorial disputes than experienced breeding pairs (Birkhead and Perrins 1986). Alternatively they may have been unable to gain sufficient weight in order to attain breeding condition due to illness or lack of food. Mathiasson (1981b) and Bacon and Coleman (1986) found that breeding birds were heavier than non-breeding birds while Reynolds (1972) determined that male swans normally required to attain a minimum weight of 10.6kg and females 8.8kg, in order to breed.

The proportions of non-territorial, territorial, breeding and non-breeding territorial swans in the Lothians total spring population for the period 1978 to 1993 were investigated in this study. During the latter years the total population increased substantially. Comparisons were made between the proportions of non-territorial, territorial, breeding and non-breeding territorial swans in the total spring population recorded during a period of low growth in swan numbers and the proportions recorded during a period of substantial growth. Comparisons were also made with results from a number of other British studies.

Few long term studies of the Mute Swan in Britain have investigated populations which increased in numbers. Hardman and Cooper (1980) described a decline in the south Warwickshire area between 1962 and 1978. Minton (1971) and Coleman et al. (1991) documented losses in the South Staffordshire population from 1961 to 1985 where the swan population declined by 40% between 1961 and 1971 and the proportion of territorial birds in the total population increased from 37% to 55% (Minton 1971). Minton (1968) noted that the ratio of non-breeding territorial pairs to territorial pairs in the South Staffordshire study area remained constant from 1961 to 1967 during which time the total population declined by 25%.

Birkhead and Perrins (1986) described the reduction in numbers on the River Thames from 1961 to 1985. Meek (1993) documented a sudden decline in swan numbers on Loch Harray and Loch Stenness, Orkney between 1990 and 1993 and Leach (1988) found the Ayrshire population to be fairly stable from 1983 to 1986. The isolated Outer Hebrides population remained stable between 1978 and 1982 (Spray 1991). The colonial breeding population at Abbotsbury in Dorset studied by Perrins and Ogilvie (1981), increased between 1968 and 1980 with a further increase being recorded in the breeding population by 1992 (Perrins et al. 1994). Numbers in the Wylye Valley, Wiltshire increased between 1978 and 1982, remained fairly constant to 1991 but declined in 1992 and 1993 (Trump et al. 1994).

Results

Total population

Prior to commencement of the present study a census of the Lothians population had been conducted only twice, in 1955 and in 1961, when each census formed a part of a census of the British population. Unfortunately, the 1961 census was only partial and no estimate was made of the total population in Scotland (Table 1).

Table 1. The Mute Swan population in spring in Scotland and in the Lothians. Data from Rawcliffe (1958), Eltringham (1963), Ogilvie (1981), Brown and Brown (1984), Brown and Brown (1985) and Brown and Brown (1993).

Year	Lothians Number of Swans	Lothians % of Base	Scotland Number of Swans	Scotland % of Base	Lothians population as % of the Scottish population
1955	215		3500-4000		5-6
1961	249		-		-
1978	116	100	3680	100	3
1983	140	121	3250	88	4
1990	275	237	4992	135	6

The Lothians population increased by 137% between 1978 and 1990 while the Scottish population increased by 35% (Table 1). Even allowing for the decline in the Scottish population between 1978 and 1983, the Scottish population increased by 54% from 1983 to 1990 and yet the Lothians population increased by 96%. These findings indicate that the percentage increase in the Lothians population was greater than the increase in the Scottish population during the present study.

The Lothians population appeared to be particularly low in 1978 relative to the Scottish population and in comparison with its size in 1961 and in 1990. In the absence of further data regarding the spring population in the intervening period 1961-1978 it was difficult to account for the low count in 1978.

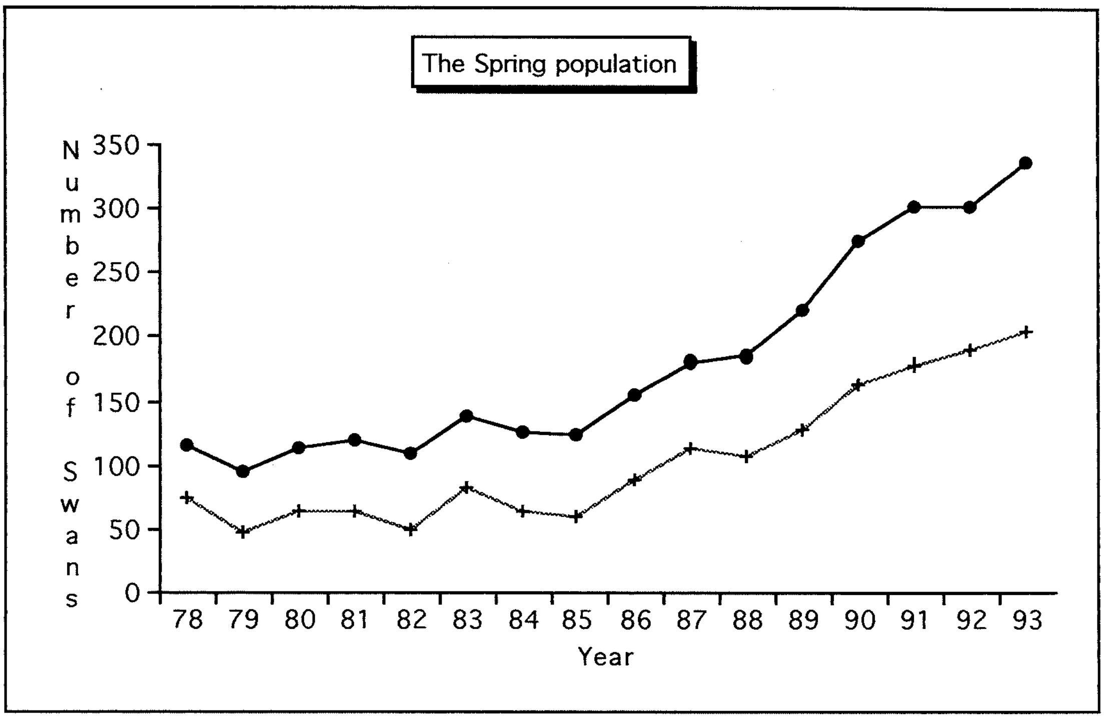


Figure 8. The total number of swans (●) and the number of non-territorial swans (+) recorded in the Lothians in April, during the period 1978 to 1993.

There was a significant increase in the number of swans in the total population from 1978 to 1993 (Spearman's Rank Correlation Coefficient, r_s =0.912, n=16, p<0.01) (Fowler and Cohen 1990) with a mean annual increase of 7%. However, the rate of increase did not appear to be consistent throughout the study period with a small rate apparent in the early ears of the study and a greater rate in later years (Figure 8). A point of change, 1985, was determined though "Broken Stick" analysis (Appendix 3). Data (Table 2) were divided into two time periods, 1978 to 1985 and 1986 to 1993, in many subsequent analyses in order to facilitate comparison of data from a period of relative stability in swan numbers with data from a period during which an upward trend was observed in swan numbers.

Table 2. The number of Mute Swans in the spring population.

Year	Total spring population	No.of non-territorial Swans	No.of occupied territories	No.of breeding pairs
1955	215	145*	-	35
1961	249	132	59	52
1978	116	76	20	15
1979	95	47	24	20
1980	115	65	26+	23
1981	121	65	28	26
1982	111	51	30	26
1983	140	84	28	26
1984	127	65	31	28
1985	124	60	32	25
1986	157	89	34	29
1987	182	114	34	32
1988	186	109	39+	34
1989	220	130	45	40
1990	275	165	55	45
1991	302	180	61	48
1992	303	189	57	50
1993	337	205	66	55
1978-85	949	513	219	189
1986-93	1962	1181	391	333
1978-93	2911	1694	610	522

* Counted in May/June

\- Not recorded

\+ The apparent discrepancies in summing the total population for 1980 and 1988 were due to two territories in 1980 being defended by single birds while in 1988 one territory was similarly occupied.

There was no significant upward trend in the total population from 1978 to 1985 ($r_s = 0.667$, $n=8$, $p>0.05$) although there was a mean annual increase of 1%. There was a significant upward trend ($r_s = 1.00$, $n=8$, $p<0.01$) from 1986 to 1993 and a mean annual increase of 12%.

Non-territorial swans

Flocks of Mute Swans were recorded at Linlithgow Loch, the River Almond Estuary at Cramond, the River Esk Estuary at Musselburgh, St.Margaret's Loch in Edinburgh, and in the vicinity of Tyninghame village (in fields, on the River Tyne and in the River Tyne Estuary) throughout the year. Maximum monthly counts (excluding territorial birds, breeding pairs and cygnets from April to September) for each of these sites for the years 1989 to 1993 were compiled in order to appraise the use of these sites relative to each other in spring and within a twelve month cycle.

The five year means of the maximum monthly counts (in some instances this was the only data available) show that these sites all held non-territorial swans in April, although no site was utilised primarily in April (Figures 9, 10 and 11). In contrast to the other sites, the number of swans at Musselburgh increased substantially between March and May (Figure 11). The May peak suggested the development of a pre-moult flock and probably included territorial swans which had failed to breed in addition to the non-territorial birds which had continued their presence from April.

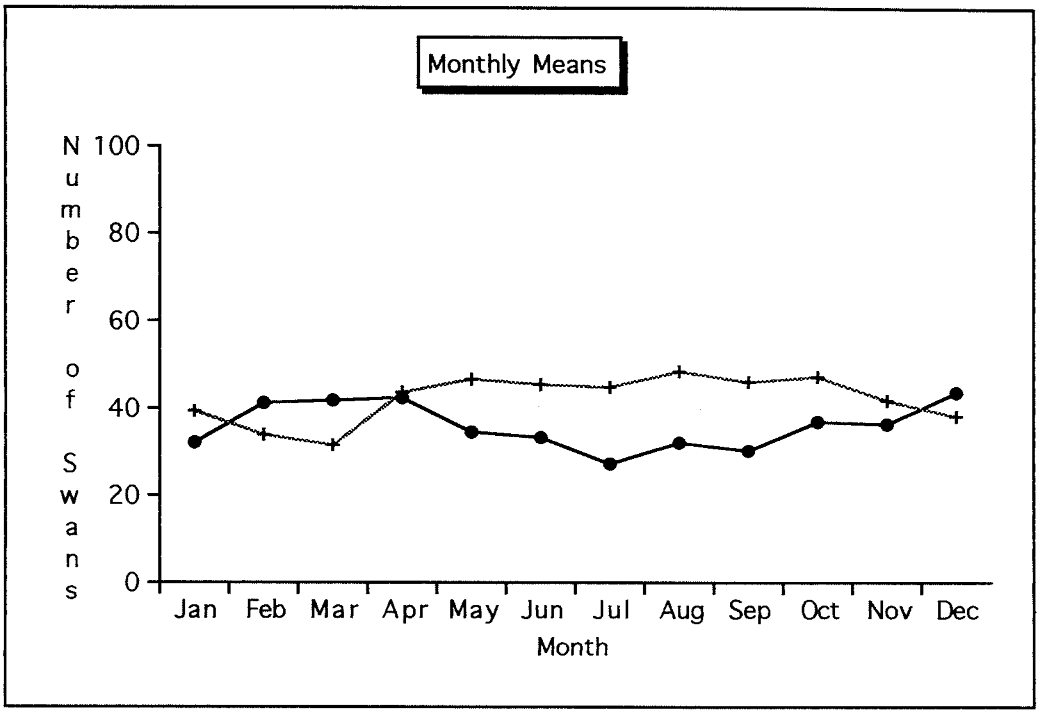


Figure 9. The monthly mean number of Mute Swans at Cramond (●) and Linlithgow Loch (+) from 1989 to 1993.

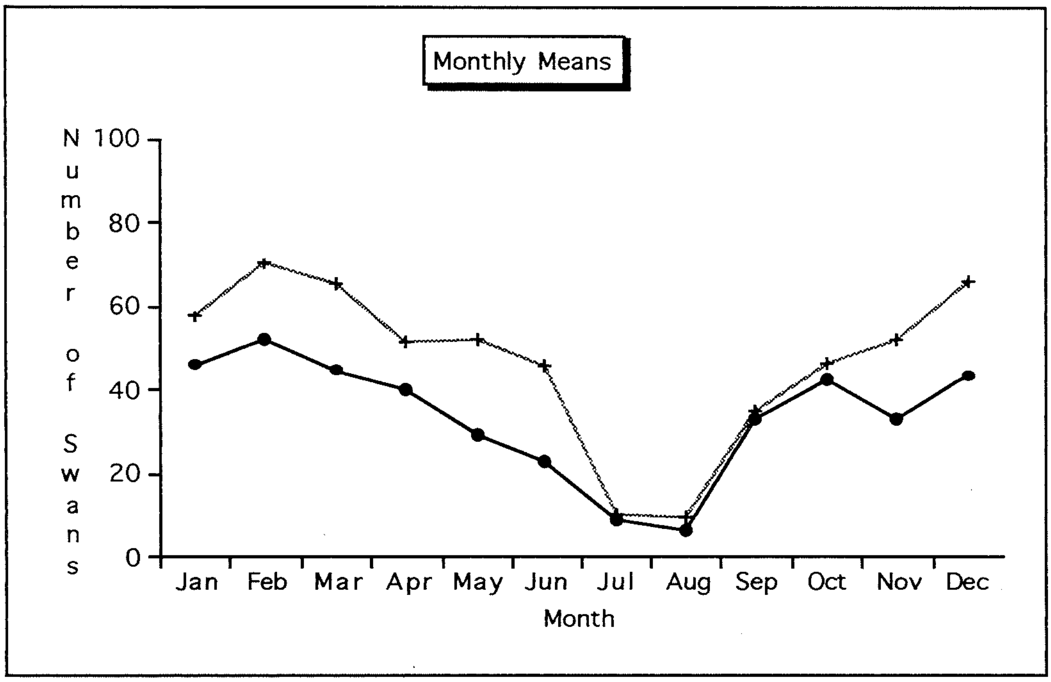


Figure 10. The monthly mean number of Mute Swans at St. Margaret's Loch (●) and Tyninghame (+) from 1989 to 1993.

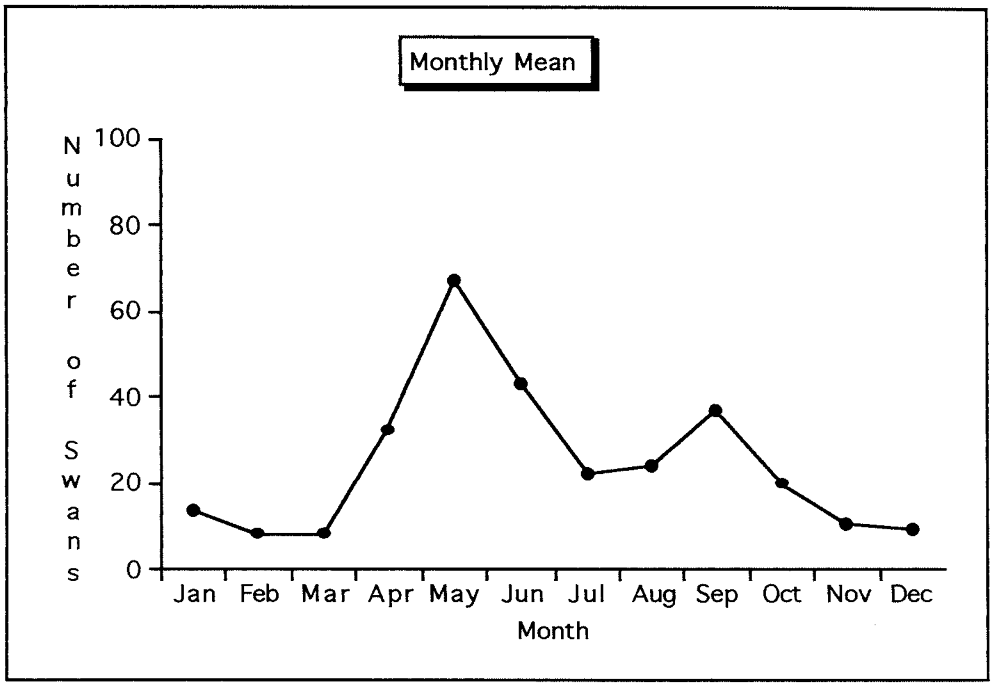


Figure 11. The monthly mean number of Mute Swans at Musselburgh from 1989 to 1993.

Mute Swans moult their flight feathers and become flightless for a period of about 40 days, between the end of May and mid October, while the new feathers are growing (Mathiasson 1973; van Dijkk and van Eerden 1991; Perrins and McCleery 1995). At that time moulting birds, especially non-territorial birds and failed breeding birds, tend to collect in flocks at sites which offer safety and a food supply. Cramond and Linlithgow Loch held a flock of moulting swans each year (Figure 9) as did Musselburgh (Figure 11). Few swans favoured St. Margaret's Loch or Tyninghame as moult sites (Figure 10).

The September peak at Musselburgh (Figure 11) resulted from swans pausing at Musselburgh while on passage between moulting and wintering sites. All five sites held a flock of swans during the winter months.

Figures 12 to 16 show that there was some annual variation in the pattern of use of each site. For example, Figure 12 shows that the peak count at Cramond in 1989 occurred in June with particularly low numbers being recorded in December whilst Figure 9 indicates numbers were generally expected to be low in June but high in December. Local bird reports frequently presented counts of Mute Swans in tables of maximum monthly counts at specified sites. It was concluded that the pattern of use of individual flock sites in the Lothians could not be determined from just one or two years of such data.

The number of swans in the total population in spring and the number of non-territorial swans increased in most years from 1989 to 1993 but this pattern of increase was not apparent from the maximum counts at individual sites in April (Figures 12 to 16).

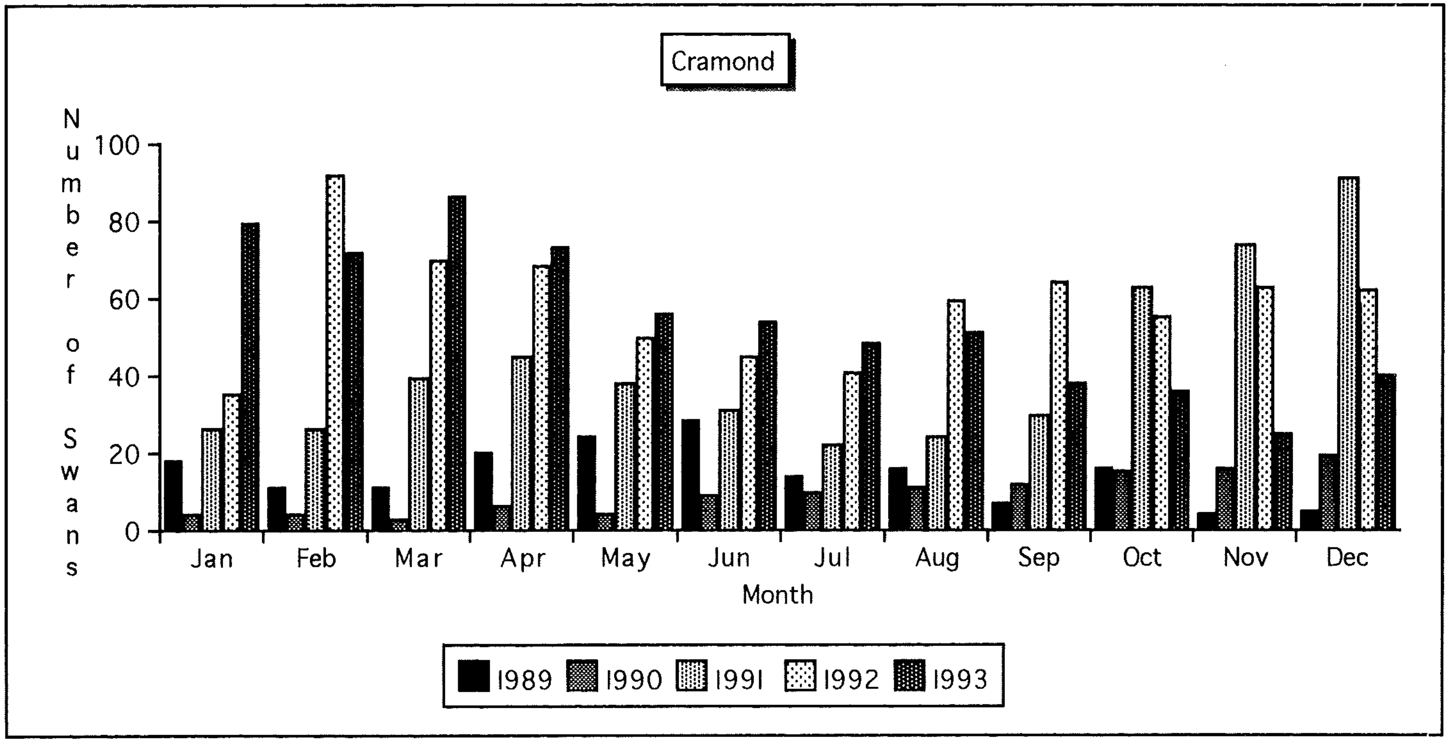


Figure 12. Maximum monthly counts at Cramond for the years 1989 to 1993.

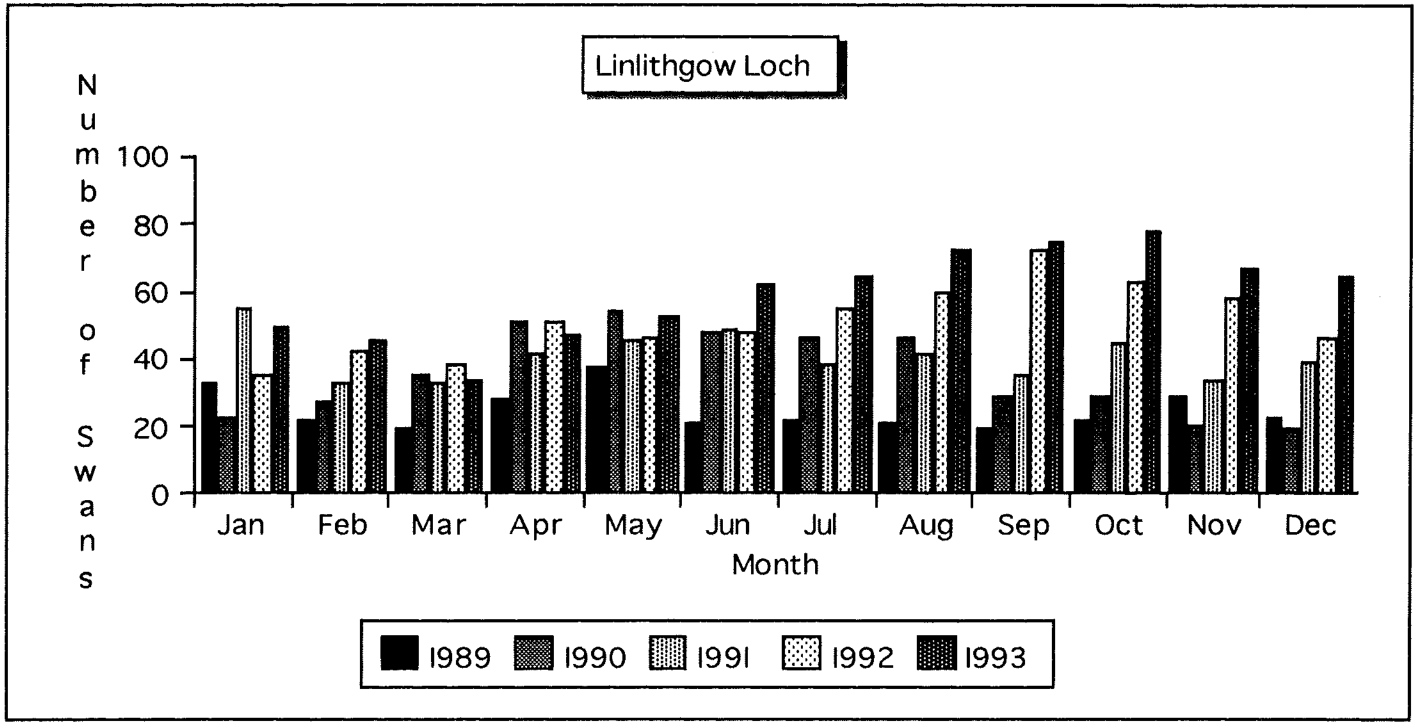


Figure 13. Maximum monthly counts at Linlithgow Loch for the years 1989 to 1993.

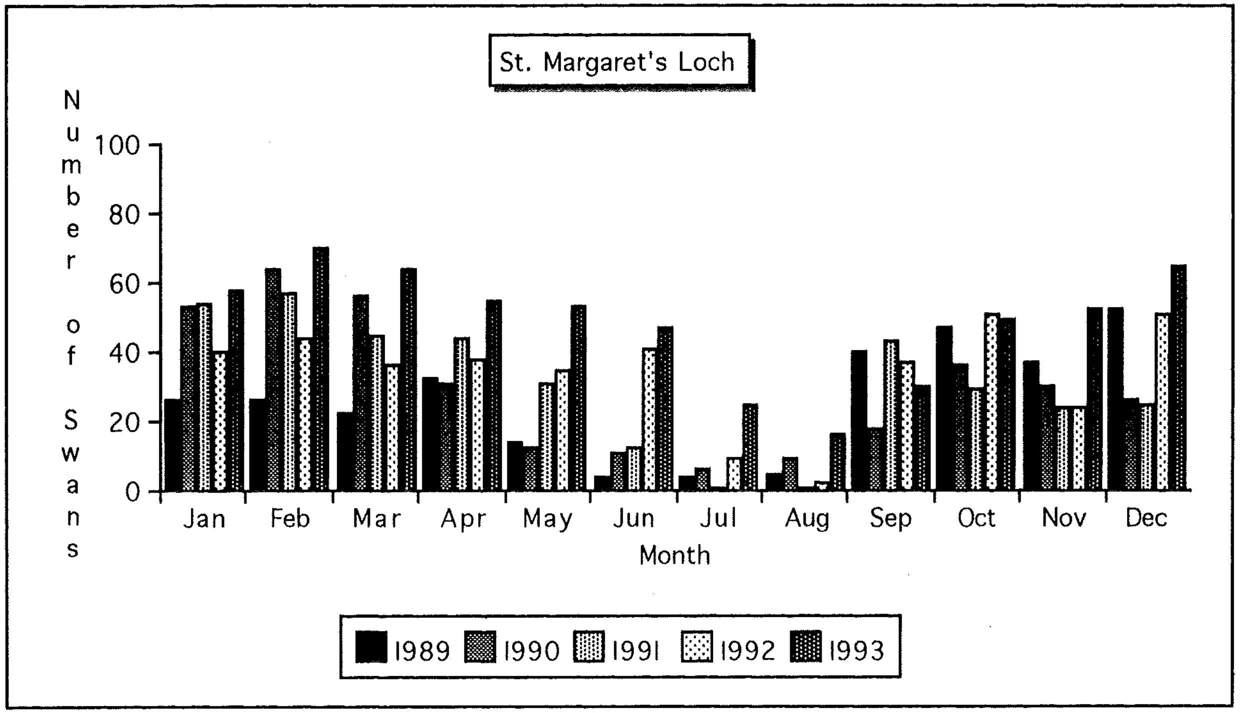


Figure 14. Maximum monthly counts at St. Margaret's Loch for the years 1989 to 1993.

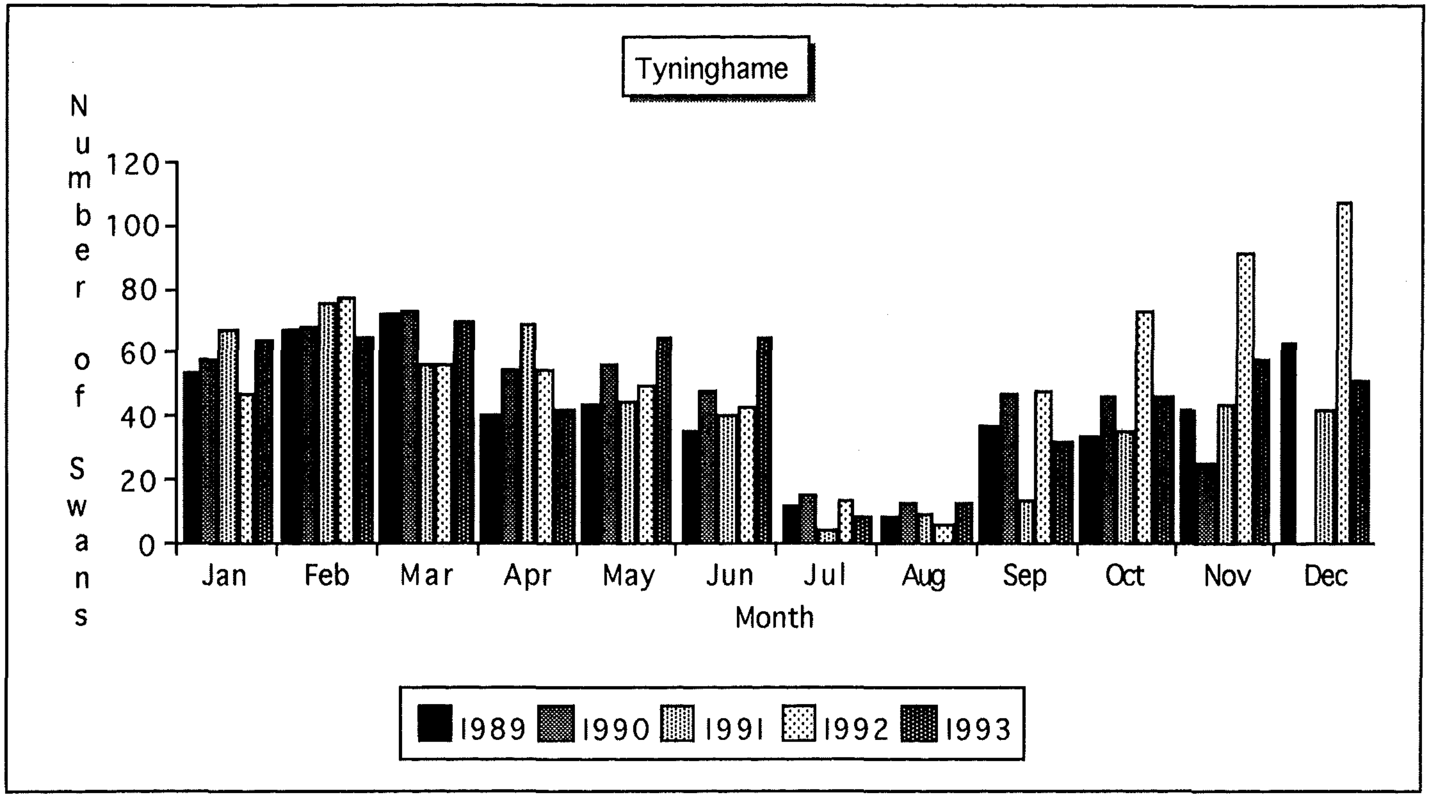


Figure 15. Maximum monthly counts at Tyninghame for the years 1989 to 1993. No counts undertaken in December 1990.

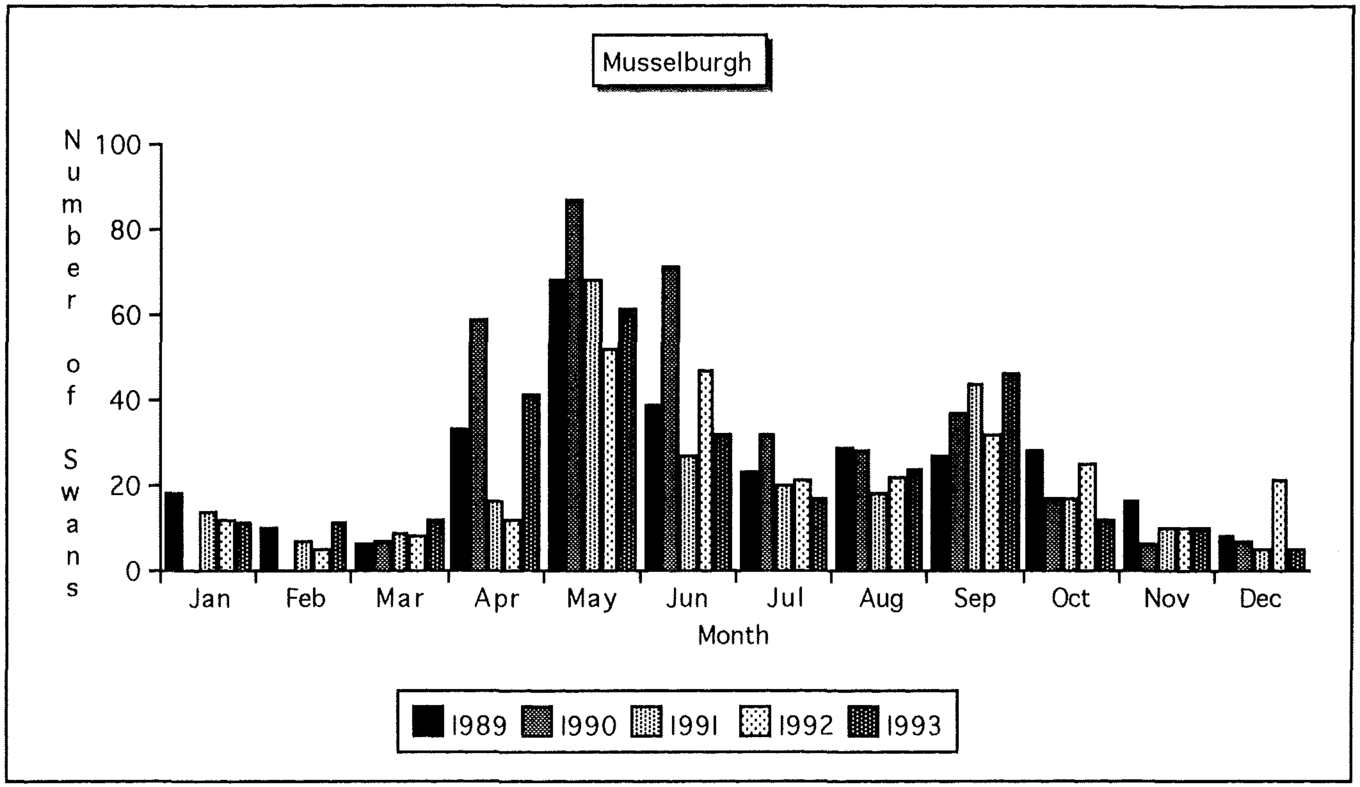


Figure 16. Maximum monthly counts at Musselburgh for the years 1989 to 1993. No counts available for January and February 1990.

The sum of monthly peak counts in April for the five principal sites for the years 1989 to 1993 did, however, show a similar trend to the total number of non-territorial swans in the Lothians population, although the former were consistently greater than the latter (Figure 17). Territorial swans were excluded from peak monthly April counts and did not account for the consistent difference, which was probably due to double counting, of individual swans which utilised a number of sites, over a period of 30 days.

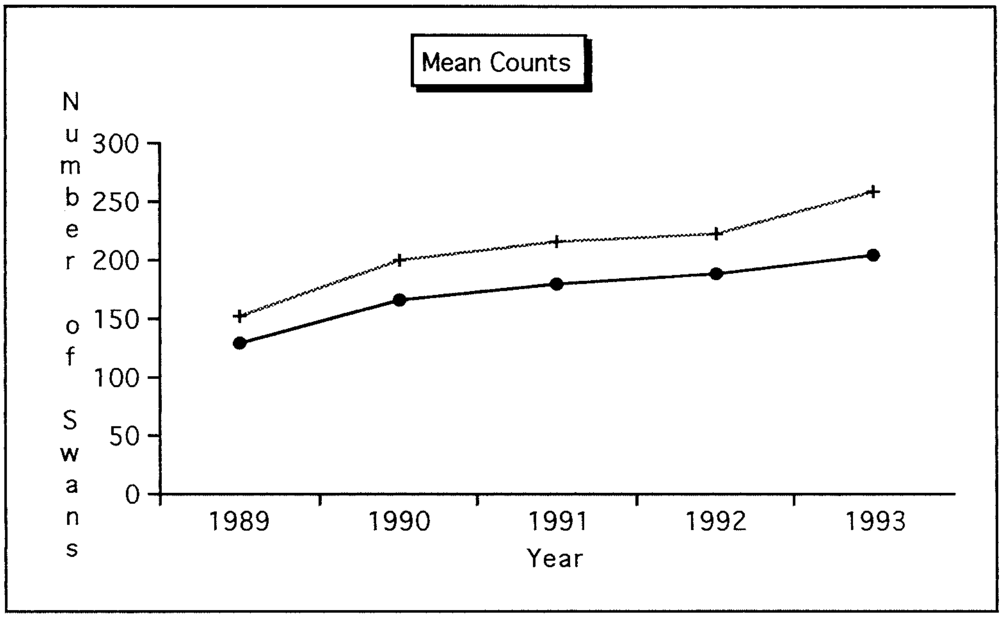


Figure 17. Total of the mean maximum counts at five principal Mute Swan sites (+) and total of non-territorial swans (●) in April, from 1989 to 1993.

Co-ordinated mid-April counts (Table 3) for each year from 1978 to 1993 show that flocks of non-territorial swans developed at Cramond, Linlithgow, Musselburgh and St. Margaret's as the number of swans in the Lothians non-territorial population increased (Figures 18 and 19).

Table 3. The number of swans in non-territorial flocks.

Year	Cramond	Linlithgow Loch	Musselburgh	St.Margaret's Loch	Tyninghame	Water of Leith
1978	0	1	3	2	59	9
1979	0	0	0	0	45	2
1980	0	0	0	0	59	6
1981	0	0	9	2	47	1
1982	0	0	15	0	19	6
1983	5	0	1	2	52	4
1984	8	0	0	9	39	0
1985	0	0	1	4	40	2
1986	0	5	1	8	52	1
1987	0	27	2	26	54	1
1988	8	14	9	26	49	0
1989	12	22	3	32	51	3
1990	4	36	21	22	73	0
1991	36	42	6	21	69	0
1992	44	41	4	38	54	0
1993	71	36	15	38	38	0

The number of swans using each site fluctuated between 1986 and 1993, in contrast to the steady increase in the overall number of non-territorial birds (Figure 8). These fluctuations, also detected in maximum monthly counts for April, may have reflected annual variations in local environmental conditions, for example food availability and the quantity of bread supplied by the public in particular.

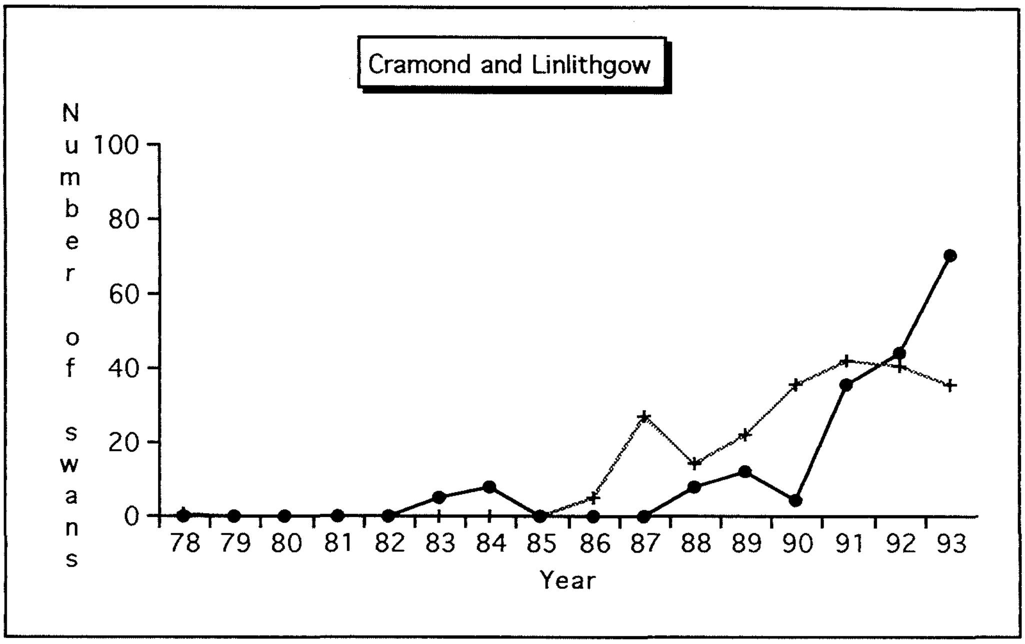


Figure 18. The number of non-territorial swans at Cramond (●) and Linlithgow Loch (+) from 1978 to 1993.

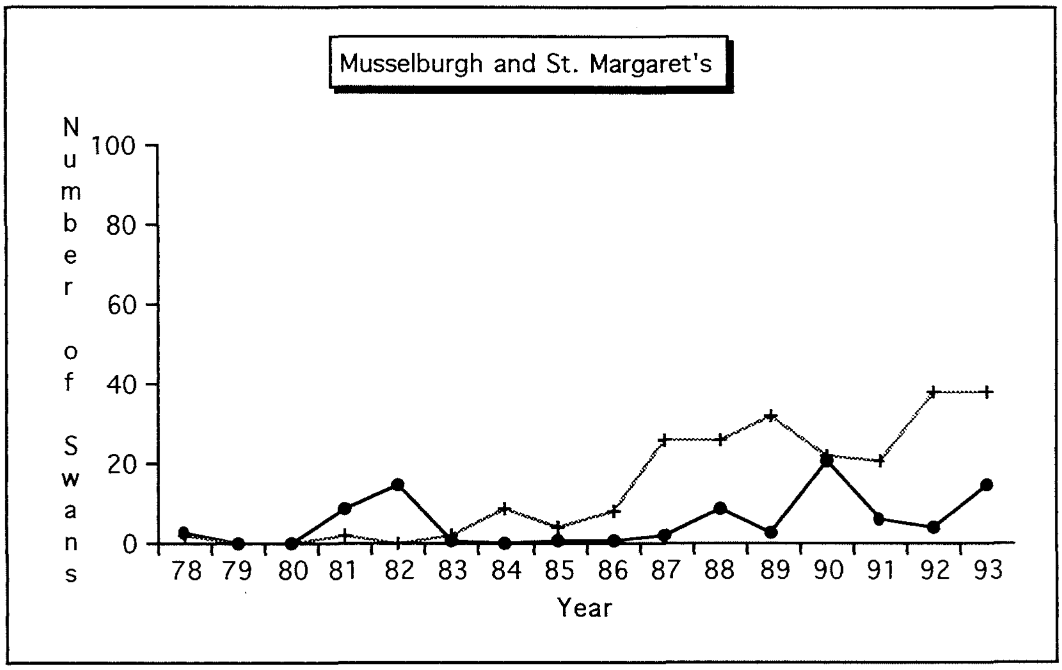


Figure 19. The number of non-territorial swans at Musselburgh (●) and St. Margarets Loch (+) from 1978 to 1993.

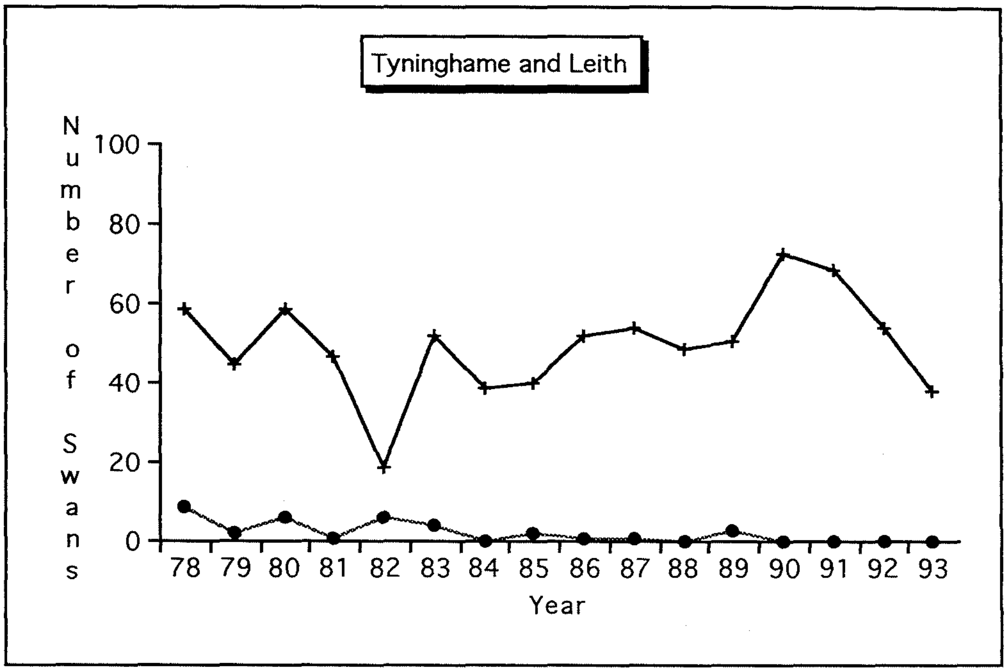


Figure 20. The number of non-territorial swans at Tyninghame (+) and Water of Leith (●) from 1978 to 1993.

The number of swans on the Water of Leith at Leith peaked at 128 birds in 1958. Construction of lock gates at the harbour entrance was completed in 1969 and precluded tidal influence within the docks and on the river at Leith. In addition, mud banks and river banks upon which swans had previously been able to preen and rest were permanently flooded and the river was lined by high walls. The number of swans utilising the area declined (A.T. McMillan pers. comm.) and few were recorded there during the present study (Figure 20).

The non-territorial flock at Tyninghame (Figure 20) did not increase in line with the increase in the total number of non-territorial birds, rather it fluctuated about a mean of 50 birds. In contrast to the other flocks, the Tyninghame flock fed in nearby fields and was not supplied with additional food by the public.

Many crops favoured by swans in winter, for example winter grown cereals, had by April grown too tall to accommodate swans. The proportion of shorter crops, for example grass, could have restricted the number of swans in the Tyninghame area as could the level of tolerance to swans exercised by farmers on whose land the preferred crops were grown. These factors may well have varied between years.

There was a mean annual decrease of 3% in the number of non-territorial swans (Figure 8) between 1978 and 1985 although this trend was not significant (r_s =0.000, n=8, p>0.05). During the period 1986 to 1993 the upward trend was significant (r_s =0.976, n=8, p<0.01) with a mean annual increase of 11%.

Throughout the study a mean of 58% of the total population comprised non-territorial birds; the mean for the period 1978 to 1985 was 54.1% (range 45.9% to 65.5%) and the mean for the period 1986 to 1993 was 60.3% (range 56.7% to 62.6%). These findings indicate an increase in the proportion of non-territorial swans in the total population and suggest that the increase in the number of non-territorial swans was greater than the increase in the number of swans in the total population.

Territorial swans

There was a significant upward trend in the number of territorial swans (Figure 21) from 1978 to 1985 (r_s =0.958, n=8, p<0.01) and from 1986 to 1993 (r_s =0.970, n=8, p<0.01) with mean annual increases during these periods of 7% and 10% respectively.

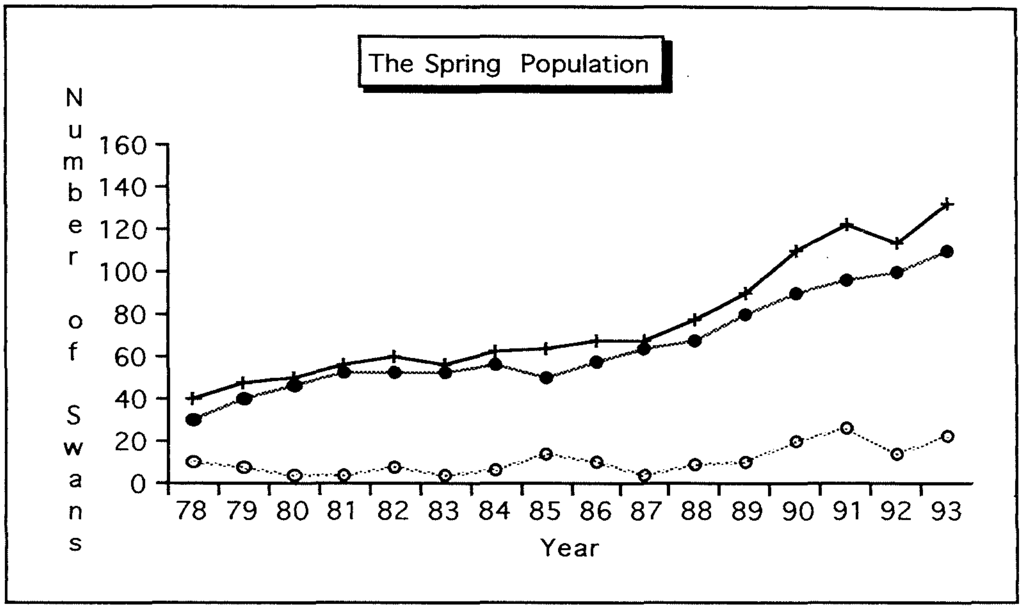


Figure 21. The number of territorial (+), breeding (●) and non-breeding territorial (o) swans in the Lothians from 1978 to 1993.

A mean of 42% of the total population was territorial during the study period; the mean for the period 1978 to 1985 was 45.9% (range 34.5% to 54.1%) and the mean for the period 1986 to 1993 was 39.8% (range 37.4% to 43.3%). These findings indicate that the territorial population declined as a proportion of the total population.

Correlation of the number of territorial swans with the number of non-territorial birds for each year from 1978 to 1985 was not significant (Product Moment Correlation Coefficient, r=-0.203, df=6, p>0.05) but was significant from 1986 to 1993 (r=0.971, df=6, p<0.01).

Breeding swans

The upward trend in the number of breeding swans (Figure 21) was significant (r_s =0.750, n=8, p<0.05) for the period 1978 to 1985 during which time the mean annual increase was

8%. A significant upward trend occurred from 1986 to 1993 (r_s=1.00, n=8, p<0.01) with a mean annual increase at that time of 10%.

Breeding birds comprised 36% of the total population from 1978 to 1993. This percentage declined during the study period since the mean for the period 1978 to 1985 was 39.8% (range 25.9% to 46.8%) and the mean for the period 1986 to 1993 was 33.9% (range 31.8% to 36.9%). Given that both the number of swans in the total population and the number of breeding swans increased between 1978 and 1993 then these findings suggest that the percentage increase in the total population there was greater than in the breeding population. This pattern contrasted with that for the non-territorial population but was similar to that for the territorial population.

The territorial population comprised 86% breeding birds from 1978 to 1993. Although the number of territorial swans and the number of breeding swans increased during the study there was little change in the mean percentage of breeding birds in the territorial population since the mean for the period from 1978 to 1985 was 86.7% (range 75.0% to 92.9%) and the mean for the period 1986 to 1993 was 85.3% (range 78.7% to 94.1%). It was concluded that the percentage increase in the number of territorial swans and the percentage increase in the number of breeding swans between the periods 1978 to 1985 and 1986 to 1993 were similar.

There was no significant correlation between the number of non-territorial birds and the number of breeding birds between 1978 and 1985 (r=-0.069, df=6, p>0.05) but the correlation was significant during the period 1986 to 1993 (r=0.981, df=6, p<0.01).

Non-breeding territorial swans

Non-breeding territorial swans (Figure 21) formed 14% of the territorial population between 1978 and 1993 and there was slight increase in that percentage between the period 1978 to 1985 (mean 13.3%, range 7.1% to 25.0%) and the period 1986 to 1993 (mean 14.7%, range 5.9% to 21.3%).

The total population comprised 5.9% non-breeding territorial birds from 1978 to 1993. There was a small decrease in that figure between the period 1978 to 1985 (mean 6.1%, range 2.9% to 11.3%) and the period 1986 to 1993 (mean 5.9%, range 2.2% to 8.6%).

Results from other British studies

The foregoing pattern of variation in the proportions of sub-sections of the total population occurred in an expanding population. Results from the present study (Table 9) are compared with the findings from five British studies for which comparable population data were available in order to establish if a common pattern of change was evident in Mute Swan populations (Table 10).

Ayrshire

There was a small increase in the total population from 1983 to 1986 (Table 4) with the number of breeding pairs remaining fairly stable (Leach 1988). There was a 72% increase in the total population and an 89% increase in the number of breeding pairs between 1986 and 1990 (Brown and Brown 1993).

Table 4. The spring population in Ayrshire.

	1983	1984	1985	1986	1990
Territorial population as % of total population	55	67	47	53	48
Breeding population as % of total population	42	56	44	40	44
Non-breeding territorial population as a % of the total population	13	11	3	14	5
% of territorial birds which bred	78	85	95	76	90
Total population	85	79	91	96	165

Analyses of the Ayrshire data for the period 1983 to 1986 revealed the total population increased by 4% per annum; between 1986 and 1990 the increase was 14% per annum. There was no significant correlation between the number of non-territorial birds and the number of territorial birds ($r=-0.703$, $df=2$, $p>0.05$) or between the number of non-territorial birds and the number of breeding birds ($r=-0.594$, $df=2$, $p>0.05$) during the period 1983 to 1986. This pattern is consistent with the pattern in the Lothians from 1978 to 1985 where there was also a small but not statistically significant increase in the total population.

<u>South Staffordshire</u>

The total population declined by 40% between 1961 and 1971 (Minton 1971), although there was no overall change in the number of breeding pairs at that time (Coleman et al.

1991). Between 1961 and 1985, however, the number of breeding pairs declined by about 50% (Coleman et al. 1991). Data comparable with that for the Lothians was available for 1961 and 1966 in Minton (1968 and 1971) (Table 5).

Table 5. The spring population in Staffordshire.

	1961	1966
Territorial population as % of total population	36	56
Breeding population as % of total population	27	41
Non-breeding territorial population as a % of the total population	9	16
% of territorial birds which bred	75	72
Total population	516	c330

Outer Hebrides

Data for the Outer Hebrides population in spring (Table 6) for the years 1978 and 1979 are from Spray (1981, Table 5). There is a discrepancy in the total population counts in Table 3 and Table 5 in Spray (1981) and between these and the data in Ogilvie (1981) for 1978. The 1983 data were extracted from Brown and Brown (1985). The total population numbered 829 birds in 1992 (Brown and Brown 1993). Breeding pairs declined from 143 in 1978, 102 in 1979 and 112 in 1983 to 80 in 1992. Thus, although Spray (1991) suggested the Hebrides population was stable, it appeared that it had declined between 1978 and 1983.

Table 6. The spring population in the Outer Hebrides.

	1978	1979	1983
Territorial population as % of total population	35	27	38
Breeding population as % of total population	31	24	33
Non-breeding territorial population as a % of the total population	4	3	6
% of territorial birds which bred	88	88	85
Total population	927	855	692

Loch Harray and Loch Stenness, Orkney.

Meek (1993) described the breakdown in territoriality and the development of colonial breeding on part of Loch Harray in 1990 when the total spring population in the loch system numbered 688 birds including 115 breeding pairs (Table 7). A large number of dead swans was recorded in 1991 but no population count was undertaken that year and by 1992 the total population numbered just 318 birds, including only 13 breeding pairs. The total population declined further to 275 birds in 1993 although the number of breeding pairs had risen to 22. The study area was comparatively small (less than 20 sq km) and the circumstances of the population crash were unusual; however the data are interesting when compared with those from other studies.

Table 7. The spring population on Loch Harray and Loch Stenness, Orkney.

	1990	1992	1993
Territorial population as % of total population	36	29	29
Breeding population as % of total population	33	8	16
Non-breeding territorial population as a % of the total population	7	72	45
% of territorial birds which bred	93	28	55
Total population	688	318	275

The Wylye Valley, Wiltshire

The total population in April (Table 8) increased between 1978 and 1982; between 1983 and 1991 there was no overall trend (Trump et al. 1994). There was no trend in the number of breeding pairs between 1978 and 1991.

Table 8. The spring population in the Wylye Valley.

	1978	1982	1983	1991
Territorial population as % of total population	73	31	22	21
Breeding population as % of total population	57	26	20	17
Non-breeding territorial population as a % of the total population	16	5	1	4
% of territorial birds which bred	78	83	95	82
Total population	63	185	176	165

Table 9. The spring population in the Lothians

	1978	1985	1986	1993
Territorial population as % of total population	34	52	43	39
Breeding population as % of total population	26	40	37	33
Non-breeding territorial population as a % of the total population	9	11	6	7
% of territorial birds which bred	75	78	85	83
Total population	116	124	157	337

Table 10 was derived from data in Tables 4 to 9 in order to facilitate comparisons between the increasing populations of Lothians (1986-1993), Ayrshire (1986-1990) and the Wylye Valley (1986-1993), and the declining Staffordshire (1961-1966), Outer Hebrides (1978-1983) and Orkney Lochs (1990-1993) populations. Data from the Lothians for the period 1978 to 1985 and for Ayrshire from 1983 to 1986 are excluded as there was no significant increase or decrease in the number of swans in the total population.

Table 10. Comparison of results from the Lothians with results from other studies. Data refer to the percentage at the beginning and end of a study period. Upward trend (+) downward trend (-); no statistical significance is implied.

	Increasing populations			Declining populations		
	Lothians	Ayrshire	Wylye	Hebrides	Stafford	Orkney
Territorial/ Total pop %	43-39	53-48	73-31	35-38	36-56	36-29
	-	-	-	+	+	-
Breeding/ Total pop %	37-33	40-44	57-26	31-33	27-41	33-16
	-	+	-	+	+	-
Non-breeding/ Total pop %	6-7	14-5	16-5	4-6	9-16	7-45
	+	-	-	+	+	+
Breeding/ Territorial %	85-83	76-90	78-83	88-85	75-72	93-55
	-	+	+	-	-	-

There was no consistent pattern between the increasing populations, between the declining populations or contrast between the increasing and declining populations (Table 10).

There was also overlap in the range of percentages recorded by expanding and declining populations, therefore no pattern could be established here either.

Habitats occupied by territorial swans

Territorial habitats in the Lothians were categorised as rivers, canals or still waters (ponds, lochs and reservoirs). The number of territories occupied during the two earlier national censuses together with data for 1978 and 1993 are shown in Table 11. Territories on rivers were proportionally significantly fewer in 1993 than in 1961 and 1978 and the proportion of pairs on still waters in 1961 was significantly lower than in 1978 and 1993 (Chi-squared = 15.91, df 4, $p<0.01$). River habitat had become less attractive to territorial Mute Swans between 1961 and 1993 while still waters became more attractive. Data for 1955 and 1956 were incomplete for rivers (Brown and Brown 1984) and were excluded from the comparison.

Table 11. Number of occupied territories in 1955, 1961, 1978 and 1993.

Habitat Type	Year	1955	1961	1978	1993
River		5	26	9	12
Canal		11	12	1	9
Still water		19	21	10	44
Total		35	59	20	65

Table 12. The number of breeding pairs in three types of habitat.

Year	Habitat Rivers	Canal	Still Waters	Total
1978	7	1	7	15
1979	8	1	11	20
1980	7	1	15	23
1981	7	1	18	26
1982	7	1	18	26
1983	8	1	17	26
1984	7	3	18	28
1985	7	2	16	25
1986	7	3	19	29
1987	6	4	22	32
1988	9	4	21	34
1989	12	2	26	40
1990	9	7	29	45
1991	8	6	34	48
1992	13	8	29	50
1993	8	9	38	55

There was a significant upward trend in the number of breeding pairs (Table 12) on still waters ($r_s = 0.948$, $n=16$, $p<0.01$), rivers ($r_s = 0.585$, $n=16$, $p<0.05$) and canals ($r_s = 0.928$, $n=16$, $p<0.01$) during the study (Figure 22).

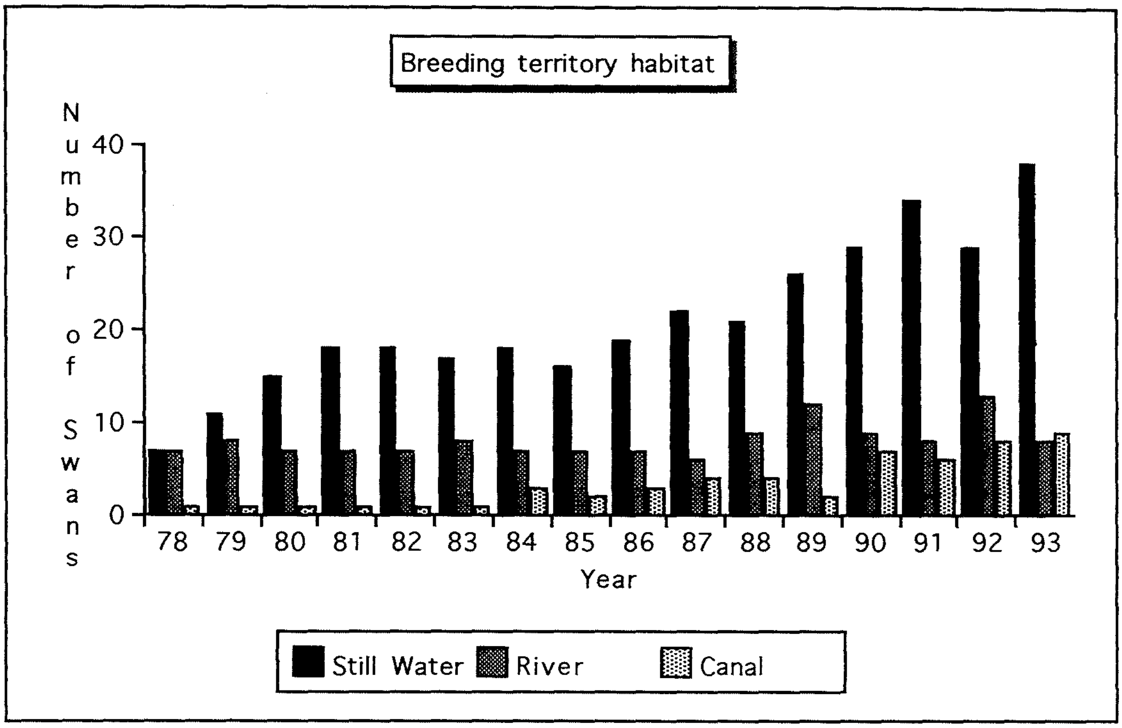


Figure 22. The number of breeding pairs in three different types of habitat.

Discussion

The reasons for the decline in the number of Mute Swans in the Lothians between 1961 and 1978 are open to speculation due to a lack of data from the intervening sixteen years. The decline involved both non-territorial and territorial birds; non-territorial birds decreased from 132 in 1961, to 76 in 1978 while the number of territorial pairs decreased from 59 to 20 (Brown and Brown 1984). The timing of the onset of the decline and the duration of the decline are unknown. Indeed, there may have been more than one period of decline with the possibility of intervening years of stability or increase.

Population indices for Mute Swans in Great Britain, calculated from autumn and winter counts, from 1960 to 1989 were determined by Kirby et al. (1994). These indicated

that, as in the Lothians, the national population declined between 1961 and 1978, with a small increase apparent by 1983 and a substantial increase by 1989. The indices indicated that, between 1960 and 1989, the national population declined from 1961 to reach a minimum value in 1970, after which there was an upward trend to 1978. Indeed, the minimum index value for south east Scotland (Lothians and Borders) was also recorded in 1970. It seemed reasonable to surmise that the number of swans in the Lothians was particularly low in the spring of 1970.
The authors indicated the decline in numbers from 1961 was primarily due to poisoning following ingestion of lead fishing weights and that the recovery in the number of swans by 1989 was due to a reduction in their use from 1982, in addition to the ban on their use implemented in 1987. There was no evidence to suggest that lead poisoning was a problem in the Lothians (Chapter 6 pp 156-158) and the ban on the use of lead fishing weights was not implemented in Scotland. Adverse weather conditions, disease or the effects of agricultural chemical sprays which drained into water bodies were among the possible causes of decline in swan numbers. By continuing the present study it should be possible to draw informed conclusions with regard to a decline in future years.

The changes which occurred as the Lothians population increased have been determined and it may be that a contrasting pattern will emerge, if and when a decline occurs. It will become apparent in the course of this project that the dynamics of the population are complex. Perhaps it was too simplistic to anticipate a clear pattern amongst increasing populations or amongst declining populations or to find a contrasting pattern between increasing and declining populations. A pattern of change may be unique to a specific study area.

There was a significant upward trend in the number of swans in the total population and in the number of non-territorial, territorial and breeding swans during the latter half of the present study while during the first half of the study period there was a significant upward trend in the number of territorial birds only. If the non-territorial flocks in the Lothians did act as a pool of birds with the potential to pair and breed in subsequent springs then a significant increase would have been anticipated in their numbers in the early stage of this study as immature birds joined the flocks prior to territorial status. This was not the case, and it may be that many birds which eventually bred in the Lothians spend their pre-breeding years outside the study area and that birds in the Lothians non-breeding flock may not breed in the Lothians. Investigations into the structure of non-territorial flocks with regard to sex ratio, age structure and proportion of Lothians hatched individuals do not form part of the present study, however it will be undertaken in the future and may help to explain the lack of association between the number of non-territorial swans and the numbers of territorial and breeding swans from 1978 to 1985. Reasons for, and causes of, the relative decline in importance of river breeding habitats will be more readily understood following analyses of pre-fledging cygnet survival in each habitat type in conjunction with an assessment of the importance of philopatry in the Lothians population.

Chapter 5

Survival of Cygnets up to the Fledging Stage

Introduction

A closed population of any species must be self-sustaining in order to survive and the individuals constituting an increase in the number of birds in a closed population must originate from within that population's boundaries. Where an increase occurs in an open population the individuals contributing to that increase could also include immigrants. Boyd and Ogilvie (1964) concluded, from ringing evidence, that closed Mute Swan populations in England were quite exceptional. Atkinson-Willes (1981) suggested the Hebrides population was virtually independent and thus constituted the only closed population in Scotland. Mute Swans were introduced to the Outer Hebrides in the latter half of the nineteenth century and Spray (1981a) believed that the population there had been self-sustaining for about one hundred years.

Results from a study of the open Mute Swan population on the River Thames from 1979 to 1982 by Birkhead and Perrins (1985) indicated that the Lower Thames swan population was not self-sustaining at that time due, in part, to high pre-fledging cygnet mortality caused by ingestion of discarded lead fishing weights.

The swan population in the Lothians study area was open and birds which contributed to the substantial population increase from 1978 to 1993 comprised both immigrants and locally hatched birds. Analysis of data regarding survival of cygnets prior to fledging constituted the first stage in the construction of a Life Table (Bacon 1980) for Mute Swans from which it would be possible to determine whether or not productivity alone accounted for the large increase in the Spring population.

Results

Pre-fledging survival of cygnets

The survival of cygnets prior to fledging on different habitats from 1981 to 1993 is shown in Table 13. The apparent inconsistency between columns in the number of cygnets recorded in a particular size category resulted from the exclusion of broods from those columns due to their temporary disappearance when the brood size could not be determined from subsequent sightings.

Table 13. Pre-fledging survival of cygnets by habitat from 1981 to 1993.

		Cygnet Survival							
		Small-medium		Medium-large		Large-fledged		Small-fledged	
Habitat									
Canals	No.of cygnets	161	144	144	140	165	164	182	155
	% survival		89%		97%		99%		85%
Rivers	No.of cygnets	280	224	227	211	214	212	299	216
	% survival		80%		93%		99%		72%
Still Waters	No.of cygnets	1059	857	876	796	850	800	1152	777
	% survival		81%		91%		94%		67%
Total	No.of cygnets	1500	1225	1247	1147	1229	1176	1633	1148
	% survival		82%		92%		96%		70%

Survival during the small size stage was greatest on canals (Chi-squared = 7.40, df 2, $p<0.05$).
Survival during the medium size stage was greatest on canals and poorest on still waters (Chi-squared = 7.11, df 2, $p<0.05$).
Survival during the large size stage was greatest on canals and rivers (Chi-squared = 16.38, df 2, $p<0.01$).
Survival from small size to fledging was greatest on canals (Chi-squared = 24.38, df 2, $p<0.01$).
The greatest losses occurred during the first few weeks post-hatching, however 70% of small cygnets survived to fledge (Table 13).

The altitudes of breeding territories ranged from 1.5m to 270m. Initially breeding territories were divided into those above or below 100m (Table 14) in order to attain a balance in the number of territories in each data group and also a balance in the altitude range in each group.

Table 14. Pre-fledging survival of cygnets hatched at different altitudes between 1981-1993.

Altitude		Cygnet Size							
		Small-medium		Medium-large		Large-fledged		Small-fledged	
1.5-100m	No. of cygnets	1186	958	969	884	935	887	1285	875
	% Survival		81%		91%		95%		68%
101-270m	No.of cygnets	314	267	278	263	294	289	348	273
	% Survival		85%		95%		98%		78%
Total	No.of cygnets	1500	1225	1247	1147	1229	1176	1633	1148
	% Survival		82%		92%		96%		70%

Results indicated there was no significant difference in survival of cygnets between the two altitude groups during the small size stage (Chi-squared = 3.14, df 1, $p>0.05$) or during the medium size stage (Chi-squared = 3.58, df 1, $p>0.05$). However, survival was greatest during the large size stage at 101m to 270m (Chi-squared = 6.84, df 1, $p<0.01$) and from the small size to fledging at 101m to 270m (Chi-squared = 14.22, df 1, $p<0.01$). These results were surprising in view of the previous results which indicated good survival on canals and rivers since canal and river breeding territories were all located below 101m. These results were further investigated by subdividing still water territories into three altitude categories (Table 15).

Table 15. Pre-fledging cygnet survival on still waters 1981-1993

Altitude		Cygnet Size							
		Small-medium		Medium-large		Large-fledged		Small-fledged	
0-50m	No.of cygnets	561	423	428	373	391	352	616	351
	% Survival		75%		87%		90%		57%
51-100m	No.of cygnets	184	167	170	160	165	159	348	273
	% Survival		91%		94%		96%		78%
101-270m	No.of cygnets	314	267	278	263	294	289	188	153
	% survival		85%		95%		98%		81%
Total	No.of cygnets	1059	857	876	796	850	800	1152	777
	% Survival		81%		91%		94%		67%

Analyses of data in Table 15 showed cygnet survival during the small size stage to be poorest in the altitude range 0m to 50m and greatest in the altitude range 51m to 100m (Chi-squared = 26.6, df 2, p<0.01).
Survival during the medium size stage was poorest in the altitude range 0m to 50m and greatest in the altitude range 101m to 270m (Chi-squared = 13.96, df 2, p<0.01).
Survival during the large size stage was poorest in the altitude range 0m to 50m and greatest in the altitude range 101m to 270m (Chi-squared = 22.63, df 2, p<0.01).
There was also a difference in survival between the altitude groups from the small stage to fledging, survival was poorest in the altitude range 0m to 50m and greatest in the altitude range 101m to 270m (Chi-squared = 66.59, df 2, p<0.01).

In the altitude category 0m to 50m, 43% of cygnets died pre-fledging with 25% being lost during the small stage. Losses were greatest during the small size stage within each still water altitudinal category.

Cygnet survival was compared between canals, rivers, still waters 0m to 50m, still waters 51m to 100m and still waters 101m to 270m.
During the small size stage cygnet survival was poorest on still waters at 0m to 50m and greatest on still waters at 51m to 100m (Chi-squared = 34.27, df 4, p<0.01).
During the medium size stage cygnet survival was poorest on still waters at 0m to 50m and greatest on canals (Chi-squared = 22.85, df 4, p<0.01).
During the large size stage cygnet survival was poorest on still water territories at 0m to 50m and greatest on rivers

(Chi-squared = 46.85, df 4, $p<0.01$).
From the small size stage to fledging, cygnet survival was poorest on still water territories at 0m to 50m and greatest on canals (Chi-squared = 94.25, df 4, $p<0.01$).

Cygnet survival to the fledging stage was poorest on still water territories below 51m with only 57% of small cygnets surviving to fledge. The greatest proportion of deaths on low altitude still waters occurred at the small cygnet stage, though mortality was relatively high during each age class.

Still water territories situated below 51m were not concentrated in one part of the study area but ranged from West Lothian through to the east of East Lothian. In addition, these sites were located in both urban and rural areas, some were open to the public while others, usually in private estates, were not. There was no evidence that vandalism was more prevalent on low altitude still waters than on the other territory classes. It was possible that the chemical content of these water bodies was dissimilar to higher altitude waters and consequently the associated vegetation differed. The vegetation may have been less abundant or not suited to the dietary requirements of developing cygnets since some pairs which failed to fledge cygnets remained in their territory and were able to obtain a food supply which was sufficient for them to survive, moult and replace their flight feathers.
In the context of the present study 57% survival appears low, however there remains the possibility that it was sufficient to sustain a population especially if post-fledging survival was high. These results should not,

therefore, be considered in isolation but compared with results from other studies and judged in combination with other demographic parameters in the breeding population.

Survival of cygnets in other areas of Britain.

Pre-fledging survival rates from four British studies are presented in Table 16. Results from the Lothians were very similar to those for the Ayrshire population where the total population had increased very slightly from 1983 to 1986 (Leach 1988) and expanded by 72% from 1986 to 1990 (Brown and Brown 1993). In South Staffordshire, where the population was in decline, pre-fledging cygnet survival was greater than in both the Lothians and Ayrshire. The low survival rate in the Oxford area in 1964 was attributed to interference from fishermen and game-keepers which was prevalent in the Oxford area in the 1960's (Bacon 1980), and to the high proportion of urban nest sites in the 1964 study area where human interference tended to be greater than in rural areas (Birkhead and Perrins 1986). The Oxford study area of Bacon (1980) from 1976 to 1978 was much larger than the earlier study area of Reynolds, was not subject to interference by fishermen and game-keepers (Bacon 1980) and included a larger proportion of rural nests; however, pre-fledging cygnet survival was poor in comparison to the Lothians, Ayrshire and South Staffordshire. More recent results from the Oxford area indicated a high survival rate. There had, however, been a substantial increase in the number of gravel pits in that study area which had been occupied by successful breeding pairs of swans (Birkhead and Perrins 1985).

On the River Thames between Oxford and Richmond there had been an unprecedented decline in the number of Mute Swans between the early 1960's and 1981 (Birkhead 1982). Lead poisoning was believed to have been the principal cause of high cygnet mortality on the lower Thames (Birkhead and Perrins 1985).

Table 16. Pre-fledging cygnet survival in Lothians and in other British studies.

Study area	Study years	Survival	Data source
Lothians	1981-1993	70% small to fledging (approx 14-16 weeks) all habitats	Present study
		85% small to fledging canals only	
		72% small to fledging rivers only	
		67% small to fledging still waters only	
Ayrshire	1983-1986	71% hatching to fledging	Leach 1988
South Staffordshire	1966-1978	76% hatching to fledging	Coleman and Minton, 1980
	1966-1985	77% hatching to fledging	Coleman et al, 1991
Oxford	1964	51% hatching to 13 weeks	Reynolds, 1965
	1964	50% hatching to 20 weeks	Perrins and Reynolds 1967
	1976-1978	53% hatching to 12 weeks	Bacon, 1980
	1980-1982	80% hatching to 10 weeks	Birkhead and Perrins, 1985
	1980-1982	79% hatching to 20 weeks	" "
Lower Thames	1980-1982	68% hatching to 10 weeks	" "
	1980-1982	46% hatching to 20 weeks	" "

Number of cygnets fledged per breeding pair in the Lothians

The number of cygnets fledged by each breeding pair from 1981 to 1993 are listed in Appendix 4. Overall, the mean number of cygnets fledged per breeding pair was 2.7. The mean number of cygnets fledged per breeding pair on rivers was significantly less than on canals (Kruskal-Wallis test, K=23.47, df 2, p<0.01). The low number of pairs on the canal (Chapter 4, Fig 22) may have contributed to the mean for rivers exceeding the mean for canals in five of the thirteen years (Table 17).

Table 17. Mean number of cygnets fledged per breeding pair on canal, river and still water territories, 1981 to 1993. (The number of breeding pair for each year are listed in Table 12, p 84)

Year	Mean no.of cygnets fledged per breeding pair		
	Canal	Rivers	Still waters
1981	5.0	2.0	2.9
1982	0.0	3.3	2.9
1983	0.0	1.3	1.1
1984	1.7	2.3	2.6
1985	3.5	3.1	3.9
1986	3.0	3.7	1.7
1987	3.5	3.8	3.1
1988	3.0	1.4	4.1
1989	5.5	1.7	3.0
1990	3.6	2.3	3.2
1991	4.5	1.8	2.3
1992	4.6	0.5	2.9
1993	2.2	1.3	2.5
Mean	3.4	2.0	2.8
95% Confidence Interval	±0.8	±0.5	±0.3

No significant trend was detected in the mean number of cygnets fledged per breeding pair each year between 1981 and 1993 on rivers (r_s =-0.442, n=13, p<0.05), canals (r_s = 0.348, n=13, p>0.05) or still waters (r_s =0.082, n=13, p>0.05).

Since cygnet mortality on rivers was not significantly lower than on the other habitats it was concluded that a larger proportion of breeding pairs on rivers than on canals failed in their breeding attempt prior to the small cygnet stage and that this factor had influenced productivity on rivers throughout the study period.

High mortality on still waters at an altitude of 0m to 50m resulted in the mean number of cygnets fledging per breeding pair in that category being significantly lower (Table 18) than on still waters in the altitude range 51m to 100m (K=28.73, df 2, p<0.01).

Table 18. Mean number of cygnets fledged per breeding pair on still waters 1981-1993.

Altitude range (m)	Number of breeding pairs	Cygnets fledged per breeding pair
		Mean
0 - 50	172	2.1
51 - 100	38	4.6
101 - 270	91	3.4

Productivity on breeding territories occupied in the latter years of the study.

A decline in the number of breeding pairs of swans in the South Midlands was accompanied by an increase in brood size at fledging between 1961 and 1978 (Coleman and Minton 1980) with a similar trend being noted on the River Thames between 1923 and 1952 (Cramp 1972). Coleman and Minton (1980) concluded that such a pattern was due to breeding pairs occupying poor breeding territories when the population was relatively numerous. If such a pattern was common to Mute Swan populations then a significant decrease in productivity would have been detected in the Lothians in the latter half of the study period or in the period 1991 to 1993 when the number of breeding pairs was greatest.

Sixteen territories on still waters in the Lothians study area were occupied by breeding pairs of swans for the first time between 1986 and 1993 (Table 19). The productivity figure for these sites from 1986 to 1993 was 2.6 cygnets fledged per breeding pair, which was marginally less than 2.7 over all still water sites from 1981 to 1985 and 2.8 over all still water sites from 1986 to 1993.

Table 19. Still water breeding territories occupied for the first time (during the present study) from 1986 to 1990* and from 1991 to 1993**.

Site	Altitude (m)	No. breeding pairs	Cygnets fledged		Cygnets fledged per breeding pair
Musselburgh Lagoon*	3	1	0		0.0
Aberlady**	1.5	1	0		0.0
Keeper's pond*	3	3	1		0.3
Markle**	30	1	0		0.0
Smeaton*	30	4	6		1.5
Lochhouses**	50	1	0		0.0
Newliston**	50	1	1		1.0
				Mean	0.7
Blackford*	90	6	16		2.7
Dalmahoy**	100	3	7		2.3
Riccarton**	100	3	14		4.7
				Mean	0.7
Dunsapie*	110	4	18		4.5
Pumpherston*	130	4	23		5.8
Garlton Hills**	140	2	7		3.5
Torbane/Half Loaf*	150	1	0		0.0
Beecraig*	150	6	12		2.0
Penicuik**	225	1	3		3.0
				Mean	3.5
Total	1986-93	42	108	Mean	2.6
	1991-93	13	31	Mean	2.4

Eight sites were occupied for the first time between 1991 and 1993. The productivity figure for those sites was 2.4 which was not significantly different from productivity of 2.5 for all remaining still water territories between 1991 and 1993 ($K=0.102$, df 1, $p>0.05$).

Comparison of the mean number of cygnets fledged per breeding pair in still water altitude categories in Table 18 with those in Table 19 suggested a decrease in productivity in recent years on territories located at 51 to 100m, although their productivity remained relatively high. Productivity on the most recently occupied sites at 0m to 50m was particularly low and suggested they were of poor quality, however the number of data was small.
It was concluded that productivity in the Lothians had not declined as the population increased nor was it low when the number of breeding pairs was particularly high between 1991 and 1993.

Productivity elsewhere in Britain.
The number of cygnets fledged per breeding pair in the Lothians and productivity results from other British studies are presented in Table 20. Productivity in the Wylye Valley ranged between 1.1 and 3.4 cygnets fledged per breeding pair and, as in the Lothians, there was no overall trend (Trump et al. 1994). Low productivity was attributed to illegal egg removal in order to reduce the numbers of Mute Swans in the area. Spray (1991) regarded the Outer Hebrides population as fairly stable. He considered it probable that a productivity figure of 1.8 cygnets fledged per breeding pair was sufficient to maintain stability in that closed population. In contrast to the situation in the

Lothians, the productivity figure for Ayrshire was low at a time when the population was in the early stages of expansion.

Table 20. The number of cygnets fledged per breeding pair in the Lothians and in other British study areas.

Study area	Years	No. of cygnets fledged per breeding pair	Data source
Lothians	1981-1993	2.7 3.4 canal 2.0 river 2.8 still water	
Ayrshire	1983-1986	1.6	Leach 1988
Hebrides	1978-1979	1.8	Spray 1981
South Staffordshire	1966-1985	2.0	Coleman et al. 1991
Wylye Valley	1978-1993	2.1	Trump et al. 1994
Oxford	1964-1966	2.0	Perrins & Reynolds 1967
	1977-1978	2.8	Bacon 1980

	1979-1982	3.8 at 20 weeks	Birkhead & Perrins 1985
Lower Thames	1979-1982	2.3 at 20 weeks	Birkhead & Perrins 1985

Productivity in South Staffordshire was higher than in both Ayrshire and the Hebrides although the Staffordshire breeding population was in decline. Birkhead and Perrins (1985) calculated that the productivity figure for the Lower Thames was too low to maintain that population. They concluded that the relatively high productivity in the Oxford area would have been insufficient to maintain the Oxford population if an increase occurred in the mortality rate of immature birds.

The overall figure for the Lothians compared well with results from these other studies and the figures for territories on the canal and still waters in the altitude groups 51m to 100m and 101m to 270m are comparatively high. Although found to be low in the context of the study, results from still waters in the altitude group 0m to 50m and rivers were not exceptionally low when compared with results from other studies. Spray (1991) also found productivity varied with habitat type from 2.9 on eutrophic lochs to 1.6 on mesotrophic lochs and 1.5 on brackish lochs.

The number of breeding pairs in the Lothians which produced cygnets

The number of breeding pairs which produced at least one small cygnet and the number of breeding pairs which fledged at least one cygnet from 1981 to 1993 on river, canal and still water habitats are presented in Tables 21, 22 and 23.

Table 21. The number of pairs of Mute Swans which bred on rivers and produced cygnets.

Year	No. Breeding Pairs	No. Pairs which produced a small cygnet	No. Pairs which fledged a cygnet
1981	7	4	4
1982	7	6	5
1983	8	3	2
1984	7	5	4
1985	7	5	5
1986	7	5	5
1987	6	5	5
1988	9	3	3
1989	12	7	5
1990	9	6	6
1991	8	7	6
1992	13	5	4
1993	8	4	3
1981-93	108	65	57

Table 22. The number of pairs of Mute Swans which bred on the canal and produced cygnets.

Year	No. Breeding Pairs	No. Pairs which produced a small cygnet	No. Pairs which fledged a cygnet
1981	1	1	1
1982	1	0	0
1983	1	0	0
1984	3	3	2
1985	2	2	2
1986	3	3	3
1987	4	4	3
1988	4	3	3
1989	2	2	2
1990	7	5	5
1991	6	5	5
1992	8	6	6
1993	9	5	5
1981-93	51	39	37

Table 23. The number of pairs of Mute Swans which bred on still waters and produced cygnets.

Year	No. Breeding Pairs	No. Pairs which produced a small cygnet	No. Pairs which fledged a cygnet
1981	18	12	11
1982	18	13	11
1983	17	8	5
1984	18	11	10
1985	16	14	13
1986	19	12	10
1987	22	19	15
1988	21	19	17
1989	26	19	16
1990	29	25	22
1991	34	24	19
1992	29	24	19
1993	38	26	23
1981-93	305	226	191

Significantly fewer breeding pairs produced a small cygnet on rivers than on canals or still waters (Chi-squared = 8.30, df 2, p<0.05). Significantly fewer breeding pairs fledged a cygnet on rivers than on canals or still waters (Chi-squared = 6.24, df 2, p<0.05). There was no significant difference between the three habitat types in the number of breeding pairs which produced at least one small cygnet and then progressed to fledge at least one cygnet (Chi-squared = 3.15, df 2, p>0.05).

These results confirm that low productivity on rivers was due to the large number of breeding pairs on rivers failing to produce any small cygnets (Figure 23). In contrast, pairs on the canal tended to produce at least one small cygnet and to fledge a cygnet (Figure 24) while the failure of many pairs on still water to loose cygnets between the small stage and fledging is apparent in Figure 25.

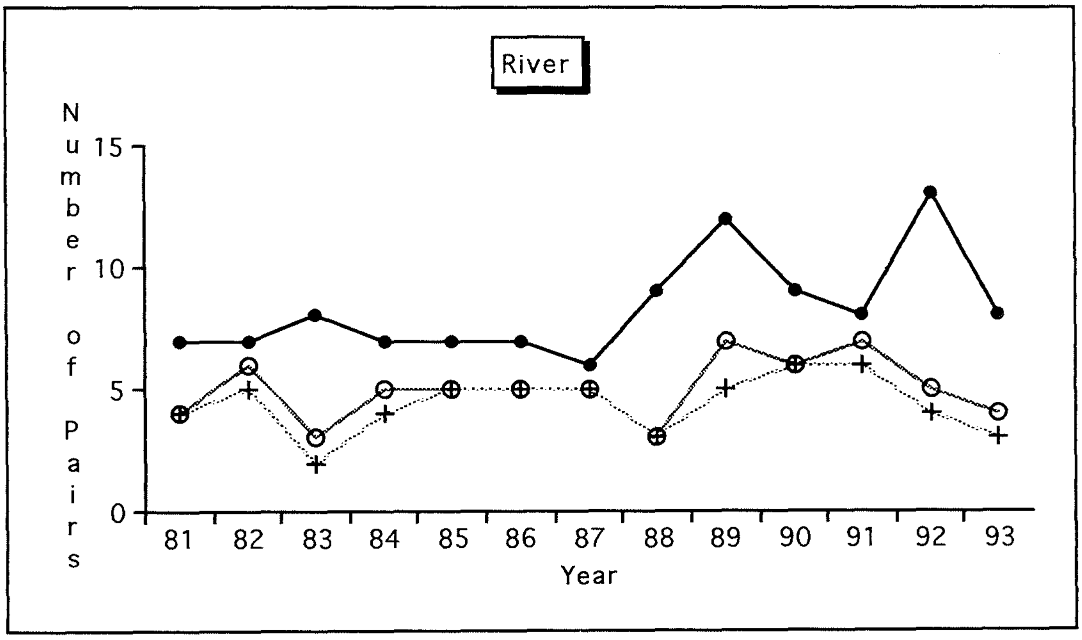


Figure 23. Numbers of breeding pairs (●) on river territories which produced a small cygnet (o) and fledged a cygnet (+) from 1981 to 1993.

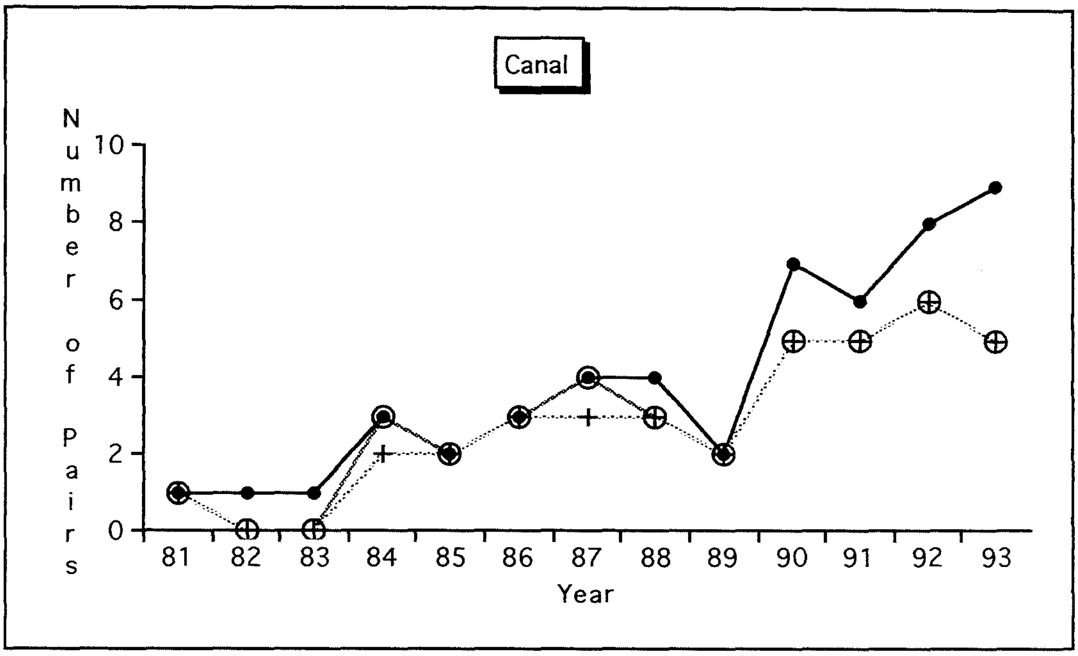


Figure 24. Numbers of breeding pairs (●) on canal territories which produced a small cygnet (o) and fledged a cygnet (+) from 1981 to 1993.

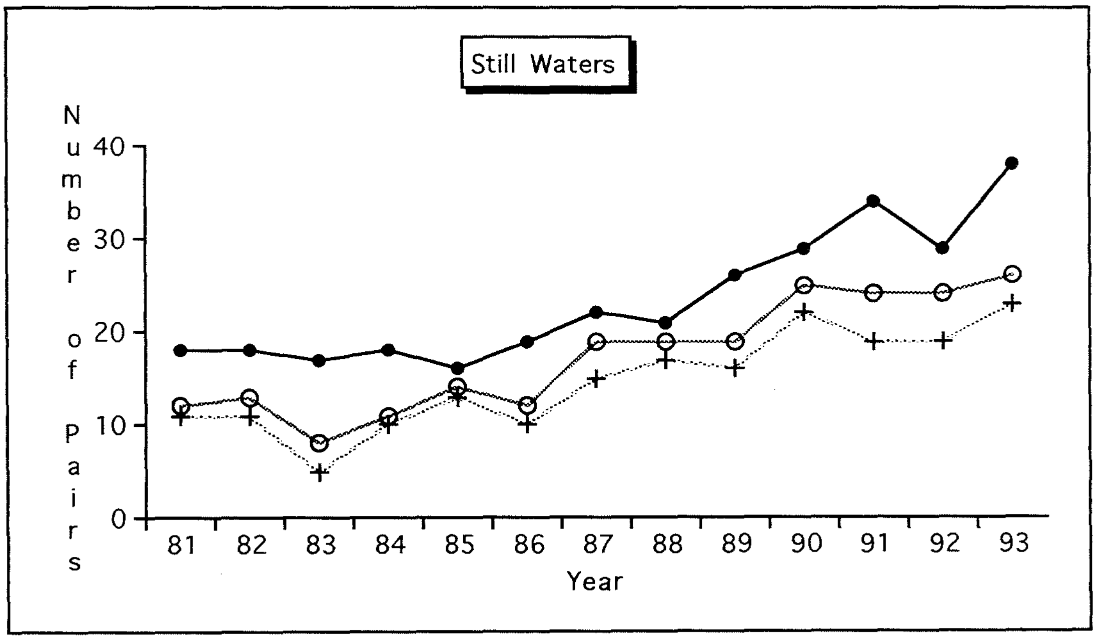


Figure 25. Numbers of breeding pairs (●) on still water territories which produced a small cygnet (o) and fledged a cygnet (+) from 1981 to 1993.

The percentage of breeding pairs which produced at least one small cygnet and the percentage of breeding pairs which fledged at least one cygnet during the study period in the three altitude groups on still waters are listed in Table 24.

Table 24. Percentage of breeding pairs which produced small cygnets and fledged cygnets from 1981 to 1993.

Habitat	No. of breeding pairs		% breeding pairs which produced a small cygnet	% breeding pairs which fledged a cygnets
Canals	51		76	73
Rivers	108		60	53
Still waters	305		74	63
Total	464	Mean	71	61
Still waters 0m-50m	172		69	54
Still waters 51m-100m	40		90	88
Still waters 101m-270m	93		76	68

Significantly more breeding pairs on still waters at 51m to 100m succeeded in producing at least one small cygnet and significantly fewer breeding pairs at 0m to 50m succeeded

in producing one small cygnet (Chi-squared = 7.40, df 2, $p<0.05$) than in the other categories of still waters. Significantly more breeding pairs which produced at least one small cygnet progressed to fledge at least one cygnet in the category 51m to 100m and significantly fewer in the altitude category 0m to 50m were successful (Chi-squared = 9.16, df 2, $p<0.05$).
Significantly more breeding pairs were successful in fledging at least one cygnet in the altitude category 51m to 100m than in the other two categories (Chi-squared = 17.10, df 2, $p<0.01$).

While low productivity on rivers was due to a greater proportion of breeding pairs failing to produce small cygnets than in other habitats it was evident that a large proportion of low altitude pairs also lost complete broods after the small cygnet stage (Table 24). However, the percentage of failures from breeding to fledging was greater on rivers than on low altitude still waters.

Association between rainfall and productivity on rivers

Water levels in the rivers were not controlled and were susceptible to fluctuation caused by rainfall, discharge from water treatment plants and extraction for agricultural use. In contrast, fluctuating water levels were not a feature of the canal territories where British Waterways controlled water flow in the canal. In 1983 and in 1993 many pairs of swans which nested on rivers failed in their breeding attempt due to flooding of their nests following high rainfall. Fluctuating water levels may also have affected the availability of aquatic vegetation to small cygnets.

During this study one breeding territory was located on the River Almond at Cramond, up to three breeding territories on the River Esk at Musselburgh and on the Water of Leith while the majority of remaining river breeding territories were located on the River Tyne.

Rainfall data were obtained for Nunraw Abbey meteorological station in East Lothian (Tables 25 and 26) in order to investigate the causes of high mortality among small cygnets on rivers. This station was chosen as the closest station to the River Tyne for which continuous rainfall measurements were available from the Meteorological Office. Few swans attempted to breed on the River Tyne above Haddington during this study although they had done so in earlier years.

Table 25. Rainfall at Nunraw Abbey, 1981 to 1993.

			Rainfall(mm)		
Year	March	April	May	3 Month Total	No. cygnets flg./ breed.pr. R.Tyne
1981	103	27	53	183	2.4
1982	51	16	58	125	4.0
1983	63	105	216	384	0.7
1984	143	20	46	209	2.4
1985	101	66	63	230	2.2
1986	31	139	63	233	4.0
1987	97	99	63	259	3.8
1988	60	49	54	163	3.0
1989	42	49	43	134	3.6
1990	19	20	31	70	3.2
1991	69	26	33	128	1.3
1992	159	49	33	241	0.7
1993	19	92	155	266	2.0
Mean (95% C.I.)	74(±27)	58(±24)	70(±33)	202(±49)	2.6±(0.7)

Table 26. Number of days in which 0.2mm and 1.0mm rainfall was recorded at Nunraw Abbey, 1981 to 1993.

	Number of days recording 0.2mm or more				Number of days recording 1.0mm or more			
Year	March	April	May	Total	March	April	May	Total
1981	23	13	18	54	8	8	13	39
1982	20	4	14	38	10	3	9	22
1983	20	20	25	65	11	13	17	41
1984	23	10	9	42	17	3	7	27
1985	18	20	15	53	14	17	9	40
1986	14	21	19	54	7	14	14	35
1987	16	13	16	45	11	8	12	31
1988	19	12	14	45	8	10	11	29
1989	15	16	11	42	8	12	8	28
1990	10	11	15	36	5	8	10	23
1991	16	16	14	46	12	8	5	25
1992	18	21	11	50	14	12	6	32
1993	11	19	13	43	6	10	10	26
Mean (95% C.I.)	17(±2)	15(±3)	15(±2)	47(±5)	11(±2)	10(±2)	10(±2)	31(±4)

There was no significant correlation between the number of cygnets fledged per breeding pair on the River Tyne and total rainfall measurements for the months of March ($r=-0.427$, $df=11$, $p>0.05$), April ($r=0.051$, $df=11$, $p>0.05$) or May ($r=-0.384$, $df=11$, $p>0.05$) for the years 1981 to 1993.

Correlation was also weak between the number of cygnets fledged on the River Tyne and the number of days in which at least 0.2mm of rainfall was recorded for the months of March ($r=-0.212$, $df=11$, $p>0.05$), April ($r=-0.514$, $df=11$, $p>0.05$) or May ($r=-0.128$, $df=11$, $p>0.05$) or the combined number of days in the three months March, April and May ($r=-0.512$, $df=11$, $p>0.05$) from 1981 to 1993.

Similarly, there was no correlation between the number of cygnets fledged per breeding pair and the number of days in which at least 1.0mm of rainfall was recorded for the months of March ($r=-0.397$, $df=11$, $p>0.05$), April ($r=-0.245$, $df=11$, $p>0.05$), May ($r=0.133$, $df=11$, $p>0.05$) or with the combined number of days in March, April and May ($r=-0.336$, $df=11$, $p>0.05$).

The possibility of correlation between this meteorological data and the proportion of breeding pairs failing to produce small cygnets was considered, since a large proportion of breeding pairs on rivers had failed by May. However, with a maximum of six breeding pairs on the River Tyne in 1983 and 1992 the annual number of breeding pairs were too few for variation in annual proportion of failures among these pairs to be meaningful in a statistical analysis.

There was, therefore, no association between these measures of rainfall and poor breeding success on the River Tyne. Nest sites on the River Esk at Musselburgh, on the River Almond at Cramond and on the River Tyne below East Linton were located in the tidal zone where high-tide patterns may have combined with heavy rainfall in some years to cause nests to be flooded.

Productivity per breeding pair from the small cygnet stage to fledging

Pre-fledging productivity in the Lothians was quite high, relative to other studies. Its sufficiency relative to the Lothians population can only be determined by its inclusion in a model including all factors involved in maintenance of the breeding population (Figure 1). Survival to the age of first breeding is one such factor and the preliminary stage in quantifying this factor is set out in Table 27.

Table 27. Productivity per breeding pair, from small cygnet stage to fledging.

Combined Habitats

Number of small cygnets produced per breeding pair		3.7
Cygnet survival small to medium size	82%	
Number of medium cygnets produced per breeding pair		3.1
Cygnet survival medium to large size	92%	
Number of large cygnets produced per breeding pair		2.8
Cygnet survival large to fledging	96%	
Number of cygnets fledged per breeding pair		2.7

Canals

Number of small cygnets produced per breeding pair		4.0
Cygnet survival small to medium size	89%	
Number of medium cygnets produced per breeding pair		3.5
Cygnet survival medium to large size	97%	
Number of large cygnets produced per breeding pair		3.4
Cygnet survival large to fledging	99%	
Number of cygnets fledged per breeding pair		3.4

Rivers

Number of small cygnets produced per breeding pair		2.7
Cygnet survival small to medium size	80%	
Number of medium cygnets produced per breeding pair		2.2
Cygnet survival medium to large size	93%	
Number of large cygnets produced per breeding pair		2.0
Cygnet survival large to fledging	99%	
Number of cygnets fledged per breeding pair		2.0

Still Waters

Number of small cygnets produced per breeding pair		4.0
Cygnet survival small to medium size	81%	
Number of medium cygnets produced per breeding pair		3.3
Cygnet survival medium to large size	91%	
Number of large cygnets produced per breeding pair		3.0
Cygnet survival large to fledging	94%	
Number of cygnets fledged per breeding pair		2.8

Still Waters in the altitude range 0m to 50m

Number of small cygnets produced per breeding pair		3.5
Survival of cygnets small to medium size	75%	
Number of medium cygnets produced per breeding pair		2.6
Survival of cygnets medium to large size	87%	
Number of large cygnets produced per breeding pair		2.3
Survival of cygnets large to fledging	90%	
Number of cygnets fledged per breeding pair		2.1

Discussion

Productivity on river and canal territories.

Low productivity by breeding pairs of swans on river territories resulted primarily from the failure of many of these pairs to produce small cygnets. It was possible that some failures resulted from nests being flooded due to a combination of high tides and substantial rainfall. Collet (1984) described the changes on a typical hydrograph for the Water of Leith following increased urbanisation in the catchment area of the river between the early 1960's and late 1970's. Similar changes undoubtedly occurred on the River Tyne following increased urbanisation at Haddington and East Linton in addition to increased efficiency in agricultural land drainage systems within the Tyne catchment area. Consequently the more rapid flow and more widely fluctuating water levels resulting from increased rainfall runoff in recent years may have caused nests to be flooded and eggs or newly hatched cygnets to be washed away, particularly if a period of substantial rainfall coincided with a high spring tide. In contrast, the water level in the Union Canal was maintained at a constant height by British Waterways, the proprietor. There were no reports of nests on the canal being flooded and relatively few breeding pairs on the canal failed to produce small cygnets.

Productivity on still waters.

Low productivity on still waters in the Lothians at 0m to 50m was primarily due to high cygnet mortality in all size categories which may have been due to an inadequate diet. Few cygnet corpses were sighted and therefore accurate determination of the cause of disappearance and death was

not possible. The cygnet corpses which were recovered had suffered from the attention of mink, foxes, crows or dogs and the cause of death could not be determined.
Spray (1991) found cygnet production in his Hebrides study area to be closely related to the type of habitat occupied by breeding swans. Eutrophic lochs were almost twice as productive as mesotrophic and brackish lochs; the difference was due largely to differential survival between hatching and fledging. The vegetation in those eutrophic lochs was extremely luxuriant and pH values exceeded 7.00.
In 1987 three breeding pairs on Bara Loch, East Lothian which normally held one breeding pair, fledged thirteen cygnets; Pressmennan Lake, which normally held two to three pairs, held four pairs and fledged twenty one cygnets in 1989. These increases in breeding pairs, combined with good productivity, were probably due to an abundance of Canadian Pondweed *Elodea canadensis* in those years.
Meek (1993) documented an increase in abundance and subsequent decline of Canadian Pondweed and the associated increase and decline in the number of Mute Swans in an Orkney loch system. Although productivity was not documented during that study the results illustrate the impact of good food supply on a swan population.
Reynolds (1972) noted significantly greater cygnet survival in territories with good surface vegetation i.e. duckweed, *Lemna species,* which was of a convenient size for small cygnets. This type of vegetation was abundant on Lothian canal territories but lacking on many low altitude still waters.

Scott and Birkhead (1983) found no association between the number of cygnets fledged and measures of territory quality. These measures included the potential amount of bread supplied and the amount and diversity of aquatic vegetation in the territory. It is possible that the actual amount of bread supplied differed from the potential amount and although the aquatic vegetation may have been high in quantity and diversity, and satisfactory for adult swans, it may have been unsuitable for cygnets. Their criteria for estimating territory quality may, therefore, have contributed to the poor correlation of territory quality and the number of young fledged in that study.

Mortality during the small cygnet stage.

Mortality in the Lothians was highest in the early post-hatching weeks with 18% loss during the small size stage, declining to 8% during the medium stage and just 4% during the large stage. In his study of Mute Swans on the west coast of Sweden, Mathiasson (1981b) also found greatest losses occurred in the first few weeks after hatching and this coincided with the period of most rapid weight gain in surviving cygnets. An adequate food supply was certainly essential at that early stage. Similar mortality patterns were determined by Leach (1988) in Ayrshire and from the results of studies in the Oxford area. Reynolds (1965), in his Oxford study during 1964, found a 31% loss during the first two weeks post hatching, 19% loss from two weeks to six weeks and a 9% loss from week six to week twelve. Also in the Oxford area but from 1976 to 1978, Bacon (1980) found that the greatest losses occurred in the first week post hatching with 17% mortality at that stage, 23% mortality in the first two weeks and 16% mortality from week two to week six.

Because mortality patterns in downy young differed in each year of his study, Bacon (1980) attributed their mortality to severe rain storms. He disagreed with the suggestion of Perrins and Reynolds (1967) that early mortality occurred when a cygnet's internal food supply (yolk sac) had been depleted and external feeding was inadequate. However, yolk sac resources last up to seven days (Owen and Black 1990) and would have been exhausted during the small cygnet stage of the present study. Since particularly wet weather would not have been confined to one type of breeding habitat it could not have caused the difference in mortality of small cygnets between the categories of breeding habitats in the Lothians. Small cygnet survival was greater on canals where small leaved floating vegetation was abundant. It is suggested, therefore, that a variation in food abundance was the principal cause of variation in cygnet mortality between habitat types at the small cygnet stage. Continuous rainfall over many days may have accentuated mortality by chilling downy young or preventing sufficient feeding time, particularly after the age of seven days. It is also possible, in addition to causing death by starvation, that an inadequate diet led to poor body condition which in turn led to greater susceptibility to fatal diseases.

There is a lack of comparable detailed information with regard to cygnet survival in relation to habitat and particularly in relation to altitude from other studies. Consequently it is difficult to determine whether good productivity in the mid-altitude, category as opposed to low and high categories, is unique to the Lothians or if it is a feature of Mute Swan populations in Scotland or indeed Britain. Similarly, it is unclear if the early failure of breeding pairs on river habitat, the high survival rate of cygnets on canal territories and the constant loss of cygnets on low altitude still waters between the small stage and fledging are unique to the Lothian.

In Ayrshire 60% of breeding failures were attributed to egg collecting (Leach 1988) while Coleman and Minton (1980) reported that half of the nests in their study area were lost due to egg stealing or vandalism in South Staffordshire from 1961 to 1978. Vandalism continued to be a major factor in that area at least up to 1985 (Coleman et al. 1991). Vandalism appeared to be sporadic and localised in the Lothians study area; although it undoubtedly affected breeding productivity it was not considered a major influence.

In addition to egg loss and cygnet mortality, the number of cygnets fledged per breeding pair was dependent upon clutch size. Scott and Birkhead (1983) and Birkhead et al. (1983) found clutch size correlated with the <u>number</u> of young fledged, although Birkhead et al. (1983) found no correlation between clutch size and the <u>proportion</u> of cygnets fledged per clutch. Clutch size was associated with laying date (pairs which produced large clutches tended to commence egg laying earlier than pairs which produced small clutches), pre-laying weight of females, winter food abundance, mean winter temperature, female genotype and previous breeding experience of pairs (Mathiasson 1981b; Scott and Birkhead 1983; Birkhead et al. 1983; Walter et al. 1991; Beekman 1991). In each of these studies winter temperature was taken as the mean for the respective study area and all breeding birds apparently remained within their respective study area throughout the winter prior to breeding.

Observations of ringed breeding birds from the Lothians suggested that some swans remained in, or in the vicinity of, their breeding territory during the winter while many vacated their breeding territory and joined flocks within the study area or dispersed throughout central and south-east Scotland and north-east England. Pairs sometimes separated for the duration of the winter and wintered in different locations while some individuals visited a number of locations within winters and varied their pattern of movement between winters.
It is possible that swans from breeding territories of high productivity dispersed in winter in a pattern which enabled them to experience higher winter temperatures and a higher quality of diet than pairs from low productivity breeding territories. This could in turn have led to larger clutches and thus greater productivity on canals and higher altitude still water breeding territories. However, the winter movements of Lothians breeding birds have not yet been investigated in sufficient detail to substantiate this possibility and it can only be suggested that a low mean clutch size on rivers and low altitude still waters may have contributed to lower productivity in those categories of breeding territory.

Lead poisoning was known to have had an impact on breeding success in the Lower Thames area but was not a problem in the Lothians (Brown and Brown 1984). Predation by animals may also have contributed to clutch and cygnet losses, however there was no indication that this was greater on rivers and low altitude still waters than on canals or other still waters.

Chapter 6

Post-fledging survival

Introduction

In order to quantify survival in a long-lived species it is necessary to mark a large proportion of the population and to monitor the survival of marked individuals over many years. These requirements were achieved in the Lothians Mute Swan study. The sex of cygnets hatched in the Lothians was determined at the time of ringing and enabled calculation of post-fledging survival rates for both sexes.

Results

Sex ratio at fledging

Cloacal examination.

Between 1982 and 1992 the sex of 614 cygnets was determined by cloacal examination (Table 28). Since examiners were more likely to be unsure of the sex of a male than a female, any bias in the ratio resulting from cloacal examination at fledging was expected to favour females.

Table 28. Number of male and female cygnets fledged from 1982 to 1992, determined by cloacal examination.

	No. cygnets fledged	No. cygnets examined male	female	indeterminate
Still water	700	256	194	22
River	194	46	34	4
Canal	147	49	35	0
Total	1041	351	263	26

There was no evidence that the ratio of males to females differed between still waters, rivers and canals (Chi-squared = 0.066, df 2, $p>0.05$).
More males (57.2%) than females (42.8%) were recorded overall (Chi-squared = 12.612, df 1, $p<0.01$). The examiners were unsure of the sex of a further 26 birds; if all 26 were females then the ratio in the 640 cygnets examined would have been significantly different; 54.8% males and 45.2% females (Chi-squared = 6.006, df 1, $p<0.05$).

In order to accommodate the possibility of a sex bias in the swan catching procedure, particularly in instances where partial broods were captured, the number of unexamined cygnets (41% of those which fledged) were considered further (Table 29). It could have been argued that, if females were generally smaller and lighter and thus more agile than males then they might have been more likely to evade capture.

Table 29. The number of cygnets which did not receive a cloacal examination.

	Total not examined	No. of complete broods not examined	No.of cygnets in in complete broods not examined
Still water	228	51	207
River	110	26	99
Canal	63	13	62
Total	401	90	368

Of the 401 birds which were not examined, 275 were not caught and 126 were caught but not examined. The majority of these swans included whole broods, 33 were from partial broods. If the proportion of males and females in the complete broods of unexamined cygnets was the same as that of the examined cygnets and all 26 'unsure' and all 33 'odd' cygnets were females, the number of males (561.5) and females (479.5) would have remained significantly different (Chi-squared = 6.459, df 1, $p<0.05$).

Reassessment of the sex of 89 birds was possible when they bred in later years. 43 birds were classed as males at fledging but 3 were later found to be females, an incorrect assessment at fledging of 7.0%. In addition, 46 cygnets were classed as females of which 1 was later identified as male, a 2.2% rate of incorrect assessment.
Application of these findings as a correction factor (Table 30) to the 614 cygnets sexed by cloacal examination resulted in 332.2 (54.1%) males and 281.8 (45.9%) females (Chi-squared = 4.138, df 1, $p<0.05$).

Table 30. The corrected percentage of male and female cygnets, determined by cloacal examination, recorded on three categories of breeding habitat from 1982 to 1992.

Breeding habitat	Males	Females
Still water	53.9%	46.1%
River	54.4%	45.6%
Canal	55.2%	44.8%
All	54.1%	45.9%

If the corrected proportion of males and females in the complete broods of unexamined cygnets was the same as that of the examined cygnets there would have been no significant difference between the number of males and the number of females only if the proportion of females in the 26 'unsure' 33 'odd' cygnets exceeded 66%.

Biometric data.

There was potential in the biometric approach for large females to be classed as males but equally small males could have been classed as females, therefore, no overall bias was anticipated.

The sex of 701 cygnets was assessed from the biometric measurements of cygnets within each brood (Table 31). The sex ratio was 52.1% male and 47.9% female with no significant difference between the number of birds in the two classes (Chi-squared = 1.200, df 1, $p>0.05$).

Table 31. Sex ratio, determined from biometric data, among cygnets fledged from 1982 to 1992.

	No. cygnets fledged	No. cygnets examined	
		male	female
Still water	700	244	228
River	194	43	45
Canal	147	78	63
Total	1041	365	336

There was no significant difference in the proportion of males and females fledged on still waters, rivers or canals (Chi-squared = 0.985, df 2, $p>0.05$).

Of the 340 birds which were not classified, 275 were not caught and 51 were caught but not measured. The remaining 14 were measured, however, they hatched later than most broods and were small at the time of capture and, although they eventually fledged, their measurements were too similar to differentiate males from females. The majority of unclassified cygnets included whole broods (Table 32) with 34 from partial broods.

If the proportion of males and females in the complete broods of unclassified cygnets was the same as that of the examined cygnets and all 34 'odd' cygnets were females, the total number of fledged cygnets would have comprised 524.4 males and 516.6 females (Chi-squared = 0.058, df 1, $p>0.05$). The outcome of this analysis would have changed only if the percentage of males in the 34 'odd' cygnets exceeded 82%.

Table 32. The number of cygnets for which sex was indeterminate from biometric data.

	Total not classified	No. of complete broods not classified	No.of cygnets in complete broods not classified
Still water	228	51	201
River	106	27	100
Canal	6	2	5
Total	340	80	306

Of 46 birds originally classed as males 3 were later found to be females and of 59 originally classed as females 4 were in fact males, giving a 6.5% incorrect assessment of males and 6.8% for females. Given that the percentages of incorrectly assessed males and females were similar no overall bias was detected in this procedure. Application of the correction factors (Table 33) to the 701 cygnets sexed from biometric data resulted in 364.1 (51.9%) males and 336.9 (48.1%) females (Chi-squared = 1.055, df 1, $p>0.05$); it was concluded that there was no significant difference in the number of males and females at fledging as determined by biometric data.

Table 33. The corrected percentage of male and female cygnets, determined by comparison of biometric data, recorded on three categories of breeding habitat from 1982 to 1992.

Breeding habitat	Males	Females
Still Water	51.6%	48.4%
River	49.2%	50.8%
Canal	54.8%	45.2%
All	51.9%	48.1%

<u>Results from other studies.</u>

Chris Spray (pers.comm.) determined the sex of 558 cygnets by cloacal examination during his study in the Hebrides from 1978 to 1982. There was strong evidence from the data that the proportion of males and females (58% males and 42% females) differed (Chi-squared = 13.88, df 1, p<0.01). Mathiasson (1981b) reported an equal proportion of males and females at fledging in the population he studied on the west coast of Sweden. Jon Coleman (pers.comm.) found slightly fewer males than females in his Northumberland study from 1991 to 1993 where 516 cygnets were sexed by cloacal examination, comprising 48% males and 52% females (Chi-squared = 0.775, df 1, p>0.05).

The number of unexamined cygnets in each of these studies was not available and correction factors were not established.

In the Thames study area during the years 1987 to 1992, 1575 cygnets were sexed by cloacal examination and a further 157 were not examined (Chris Perrins, pers.comm.). Of those which were examined, significantly more (53.7%) were classed as males (Chi-squared = 8.691, df 1, $p<0.01$). The proportion of males and females in the fledged population would have been similar if the 157 unexamined cygnets comprised at least 61% females.

Since correction factors were not established in any of the above studies and the number of unexamined cygnets was not available for most of the studies it was difficult to determine whether the tendency towards more males was real or if the sexes did in fact occur in equal proportions. It was noted that none of the other studies, nor the Lothians study, reported a significantly greater proportion of females than males.

A decision was required to be made by the cloacal examiner in the field at a time when the examiner may have been under pressure to make a quick assessment due, for instance, to inclement weather. Recording of biometric data in the field enabled a more considered assessment to be made of the sex of cygnets based on information available on each brood, including time of hatching, breeding site etc. at a later time.

Proportion of fledged cygnets which were colour ringed.

The proportion of fledged cygnets which were ringed during the study required to be quantified in order to calculate further demographic parameters, such as immigration, in

Chapter 7. Wet weather in the spring of 1983 resulted in just seven pairs of swans fledging cygnets; in addition permission had not been received from landowners to ring two large broods hence the low percentage of fledged cygnets which were colour ringed in 1983 (Table 34.).

Table 34. Percentage of fledged cygnets colour ringed from 1982 to 1993.

Year	No. Fledged	% Colour Ringed
1982	75	76.0
1983	28	32.1
1984	67	79.1
1985	91	62.3
1986	68	69.1
1987	106	67.0
1988	110	78.2
1989	109	70.1
1990	139	84.9
1991	118	88.1
1992	128	83.6
1993	129	83.7

During the period 1982 to 1993, 76.5% of cygnets which fledged were colour ringed. Additionally, the mean number of cygnets which fledged and were colour ringed during the following periods were calculated for use in Chapter 7.

· 1982 to 1989	mean	69.9%
· 1982 to 1990	"	72.5%
· 1982 to 1991	"	74.6%
· 1982 to 1992	"	75.6%.

Prior to 1990, permission was not granted to catch and ring swans on the River Tyne below Tyninghame nor in the John Muir Country Park in East Lothian. Consequently, broods which had been raised in that area and broods which moved down river and into the Tyne Estuary by the autumn were not ringed. Therefore, proportionately fewer river cygnets were ringed prior to 1990.

In comparison, Coleman and Minton (1979) ringed an average of 66% of the cygnets which fledged in South Staffordshire from 1961 to 1975. The percentage of cygnets which they ringed increased as the study progressed with over 80% of fledged cygnets being ringed after 1970.

Age-specific Survival

There are numerous statistical difficulties involved in modelling survival rates of bird populations from ringing data, particularly amongst young birds (Newton et al. 1983; Brownie et al. 1985), and in determining significant differences in survival rates between years and between age classes (Perrins 1991b; Harris et al. 1994a; Harris et al.

1994b).

An assumption of constant survival, required in some models, could not be justified for Mute Swans in Britain since survival was low amongst young swans, increasing in later years (Perrins 1991b) with the possibility of a terminal decline in the last years (Newton 1989b). In addition, data on survival between years and between age classes were not independent, for example an individual which survived to age three years would also have been recorded in the first and second year age class data. Prior to the early 1980's, the life table model had been widely employed to determine survival rates in animal populations. The life table was dependent on a number of assumptions which Anderson et al. (1981) contend could not be fulfilled by the data collected from many ornithological ringing schemes. Survival rates calculated using the life table model were shown by Burnham and Anderson (1979) and Anderson et al. (1985) to be inaccurate for ornithological data.

A number of assumptions inherent in some other survival estimation models (Newton 1986) can be reasonably justified for the Lothians Mute Swan study -

- A large proportion of cygnets fledged in the Lothians were ringed, thus the ringed birds were considered to be representative of the Lothians population.

- There was no evidence that ringing affected survival. Chris Spray (pers. comm.) suggested that the use of coloured neck collars on Mute Swans in the Hebrides made such ringed individuals more susceptible than non-collared individuals to being shot. Survival rates in such ringing schemes, therefore, may not be independent of a ringing effect. The level of deliberate shooting of swans ringed in the Lothians was considered to be insignificant.

- Once ringed, an individual was ringed for life. The number of swans which simultaneously lost both colour ring and metal ring was inconsequential.

- The chance of the digits on a colour ring being read or the ringed bird being recovered dead was not considered to be dependent upon the age of an individual.

The estimates of survival for swans which were ringed and fledged in the Lothians were based on the number of swans which survive from the beginning of one year to the beginning of the next year. A few swans aged at least eleven years were known to have bred in the Lothians in recent years. These birds were ringed prior to the commencement of the present study and since it was probable that a number of swans ringed during the study would survive also beyond the age of 11 years the data in Tables 35 to 43 were truncated at the 11th age class. As the age class progressively increased so the number of years in which cygnets fledged progressively decreased and the number of data decreased sequentially through Tables 35 to 43.

The notation used in Tables 35 to 43 was suggested by Professor G. Raab (pers. comm.) and is as follows :-

n1 = number at start of 1st year
s1 = number surviving 1st year
d1 = number dying in 1st year [n1-s1]
e1 = expected number of deaths in 1st year if survival of all groups is the same n1(1-P1) - see below for definition of P1
p1 = proportion surviving 1st year [s1/n1]

n2 = number at start of 2nd year
s2 = number surviving 2nd year
etc. etc. to 11th year

Column Totals
N1, S1, D1 are sums of the above
P1 = (S1 males + S1 females)/(N1 males + N1 females)
etc. etc. to 11th year

Table 35. Survival during the first year after fledging.

Year Fledged	Sex	n1	s1	d1	e1	p1
1982	m	27.00	18.00	9.00	8.16	0.67
	f	30.00	20.00	10.00	9.06	0.67
1983	m	5.00	3.00	2.00	1.51	0.60
	f	4.00	3.00	1.00	1.21	0.75
1984	m	23.00	17.00	6.00	6.95	0.74
	f	30.00	16.00	14.00	9.06	0.53
1985	m	30.00	23.00	7.00	9.06	0.77
	f	27.00	20.00	7.00	8.16	0.74
1986	m	22.00	19.00	3.00	6.65	0.86
	f	20.00	19.00	1.00	6.04	0.95
1987	m	44.00	27.00	17.00	13.29	0.61
	f	27.00	20.00	7.00	8.16	0.74
1988	m	53.00	37.00	16.00	16.01	0.70
	f	30.00	25.00	5.00	9.06	0.83
1989	m	43.00	29.00	14.00	12.99	0.67
	f	34.00	20.00	14.00	10.27	0.59
1990	m	63.00	44.00	19.00	19.03	0.70
	f	55.00	39.00	16.00	16.61	0.71
1991	m	57.00	44.00	13.00	17.22	0.77
	f	47.00	28.00	19.00	14.20	0.60
1992	m	67.00	42.00	25.00	20.24	0.63
	f	40.00	30.00	10.00	12.08	0.75
Total		N1	S1	D1		P1
	m	434.00	303.00	131.00		0.70
	f	344.00	240.00	104.00		0.70
	m+f	778.00	543.00	235.00		0.70

Survival (S1/N1*100)		Survival from fledging (P1*100)	
m	70 %	m	70 %
f	70 %	f	70 %
m+f	70 %	m+f	70 %

Table 36. Survival during the second year after fledging.

Year Fledged	Sex	n2	s2	d2	e2	p2
1982	m	18.00	17.00	1.00	3.90	0.94
	f	20.00	14.00	6.00	4.33	0.70
1983	m	3.00	1.00	2.00	0.65	0.33
	f	3.00	3.00	0.00	0.65	1.00
1984	m	17.00	12.00	5.00	3.68	0.17
	f	16.00	14.00	2.00	3.46	0.88
1985	m	23.00	18.00	5.00	4.98	0.78
	f	20.00	14.00	6.00	4.33	0.70
1986	m	19.00	13.00	6.00	4.11	0.68
	f	19.00	16.00	3.00	4.11	0.84
1987	m	27.00	24.00	3.00	5.85	0.89
	f	20.00	18.00	2.00	4.33	0.90
1988	m	37.00	35.00	2.00	8.01	0.95
	f	25.00	22.00	3.00	5.41	0.88
1989	m	29.00	24.00	5.00	6.28	0.83
	f	20.00	14.00	6.00	4.33	0.70
1990	m	44.00	30.00	14.00	9.53	0.68
	f	39.00	33.00	6.00	8.45	0.85
1991	m	44.00	30.00	14.00	9.53	0.68
	f	28.00	17.00	11.00	6.06	0.61
Total		N2	S2	D2		P2
	m	261.00	204.00	57.00		0.78
	f	210.00	165.00	45.00		0.79
	m+f	471.00	369.00	102.00		0.78

Survival (S2/N2*100)		Survival from fledging (P1*P2*100)	
m	78 %	m	55 %
f	79 %	f	55 %
m+f	78 %	m+f	55 %

Table 37. Survival during the third year after fledging.

Year Fledged	Sex	n3	s3	d3	e3	p3
1982	m	17.00	14.00	3.00	3.64	0.82
	f	14.00	9.00	5.00	3.00	0.64
1983	m	1.00	0.00	1.00	0.21	0.00
	f	3.00	1.00	2.00	0.64	0.33
1984	m	12.00	9.00	3.00	2.57	0.75
	f	14.00	13.00	1.00	3.00	0.93
1985	m	18.00	10.00	8.00	3.86	0.56
	f	14.00	12.00	2.00	3.00	0.86
1986	m	13.00	11.00	2.00	2.79	0.85
	f	16.00	14.00	2.00	3.43	0.88
1987	m	24.00	20.00	4.00	5.14	0.83
	f	18.00	15.00	3.00	3.86	0.83
1988	m	35.00	31.00	4.00	7.50	0.89
	f	22.00	17.00	5.00	4.71	0.77
1989	m	24.00	19.00	5.00	5.14	0.79
	f	14.00	10.00	4.00	3.00	0.71
1990	m	30.00	26.00	4.00	6.43	0.87
	f	33.00	22.00	11.00	7.07	0.67
Total		N3	S3	D3		P3
	m	174.00	140.00	34.00		0.80
	f	148.00	113.00	35.00		0.76
	m+f	322.00	253.00	69.00		0.79

Survival (S3/N3*100)		Survival from fledging (P1*P2*P3*100)	
m	80 %	m	44 %
f	76 %	f	42 %
m+f	79 %	m+f	43 %

Table 38. Survival during the fourth year after fledging.

Year Fledged	Sex	n4	s4	d4	e4	p4
1982	m	14.00	9.00	5.00	2.87	0.64
	f	9.00	7.00	2.00	1.84	0.78
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.20	1.00
1984	m	9.00	7.00	2.00	1.84	0.78
	f	13.00	12.00	1.00	2.66	0.92
1985	m	10.00	7.00	3.00	2.05	0.70
	f	12.00	7.00	5.00	2.46	0.58
1986	m	11.00	9.00	2.00	2.25	0.82
	f	14.00	12.00	2.00	2.87	0.86
1987	m	20.00	16.00	4.00	4.10	0.80
	f	15.00	10.00	5.00	3.07	0.67
1988	m	31.00	26.00	5.00	6.35	0.84
	f	17.00	15.00	2.00	3.48	0.88
1989	m	19.00	16.00	3.00	3.89	0.84
	f	10.00	9.00	1.00	2.05	0.90

Total		N4	S4	D4		P4
	m	114.00	90.00	24.00		0.79
	f	91.00	73.00	18.00		0.80
	m+f	205.00	163.00	42.00		0.80

Survival (S4/N4*100)		Survival from fledging (P1*P2*..P4*100)	
m	79 %	m	35 %
f	80 %	f	34 %
m+f	80 %	m+f	35 %

Table 39. Survival during the fifth year after fledging.

Year Fledged	Sex	n5	s5	d5	e5	p5
1982	m	9.00	8.00	1.00	1.89	0.89
	f	7.00	5.00	2.00	1.47	0.71
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.21	1.00
1984	m	7.00	4.00	3.00	1.47	0.57
	f	12.00	11.00	1.00	2.52	0.92
1985	m	7.00	5.00	2.00	1.47	0.71
	f	7.00	6.00	1.00	1.47	0.86
1986	m	9.00	8.00	1.00	1.89	0.89
	f	12.00	11.00	1.00	2.52	0.92
1987	m	16.00	13.00	3.00	3.36	0.81
	f	10.00	8.00	2.00	2.10	0.80
1988	m	26.00	19.00	7.00	5.46	0.73
	f	15.00	10.00	5.00	3.15	0.67

Total		N5	S5	D5		P5
	m	74.00	57.00	17.00		0.77
	f	64.00	52.00	12.00		0.81
	m+f	138.00	109.00	29.00		0.79

Survival (S5/N5*100)		Survival from fledging (P1*P2*..P5*100)	
m	77 %	m	27 %
f	81 %	f	27 %
m+f	79 %	m+f	27 %

Table 40. Survival during the sixth year after fledging.

Year Fledged	Sex	n6	s6	d6	e6	p6
1982	m	8.00	7.00	1.00	1.60	0.88
	f	5.00	4.00	1.00	1.00	0.80
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.20	1.00
1984	m	4.00	4.00	0.00	0.80	1.00
	f	11.00	11.00	0.00	2.20	1.00
1985	m	5.00	3.00	2.00	1.00	0.60
	f	6.00	6.00	0.00	1.20	1.00
1986	m	8.00	5.00	3.00	1.60	0.62
	f	11.00	8.00	3.00	2.20	0.73
1987	m	13.00	10.00	3.00	2.60	0.77
	f	8.00	5.00	3.00	1.60	0.62

Total		N6	S6	D6	P6
	m	38.00	29.00	9.00	0.76
	f	42.00	35.00	7.00	0.83
	m+f	80.00	64.00	16.00	0.80

Survival	(S6/N6*100)	Survival from fledging (P1*P2*...P6*100)	
m	76 %	m	20 %
f	83 %	f	23 %
m+f	80 %	m+f	22 %

Table 41. Survival during the seventh year after fledging.

Year Fledged	Sex	n7	s7	d7	e7	p7
1982	m	7.00	7.00	0.00	1.14	1.00
	f	4.00	3.00	1.00	0.65	0.75
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.16	1.00
1984	m	4.00	4.00	0.00	0.65	1.00
	f	11.00	9.00	2.00	1.80	0.82
1985	m	3.00	3.00	0.00	0.49	1.00
	f	6.00	5.00	1.00	0.98	0.83
1986	m	5.00	3.00	2.00	0.82	0.60
	f	8.00	6.00	2.00	1.31	0.75

Total		N7	S7	D7		P7
	m	19.00	17.00	2.00		0.89
	f	30.00	24.00	6.00		0.80
	m+f	49.00	41.00	8.00		0.84

Survival (S7/N7*100)

m	89 %
f	80 %
m+f	84 %

Survival from fledging (P1*P2*..P7*100)

m	18 %
f	18 %
m+f	18 %

Table 42. Survival during the eighth and ninth years after fledging.

Year Fledged	Sex	n8	s8	d8	e8	p8
1982	m	7.00	5.00	2.00	1.53	0.71
	f	3.00	3.00	0.00	0.66	1.00
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.22	1.00
1984	m	4.00	3.00	1.00	0.88	0.75
	f	9.00	7.00	2.00	1.97	0.78
1985	m	3.00	3.00	0.00	0.66	1.00
	f	5.00	3.00	2.00	1.09	0.60
Total		N8	S8	D8		P8
	m	14.00	11.00	3.00		0.79
	f	18.00	14.00	4.00		0.78
	m+f	32.00	25.00	7.00		0.78

	Survival (S8/N8*100)		Survival from fledging (P1*P2*..P8*100)
m	79 %	m	14 %
f	78 %	f	14 %
m+f	78 %	m+f	14 %

Year Fledged	Sex	n9	s9	d9	e9	p9
1982	m	5.00	3.00	2.00	0.79	0.60
	f	3.00	3.00	0.00	0.47	1.00
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	1.00	0.00	0.16	1.00
1984	m	3.00	3.00	0.00	0.47	1.00
	f	7.00	6.00	1.00	1.11	0.86
Total		N9	S9	D9		P9
	m	8.00	6.00	2.00		0.75
	f	11.00	10.00	1.00		0.91
	m+f	19.00	16.00	3.00		0.84

	Survival (S9/N9*100)		Survival from fledging (P1*P2*..P9*100)
m	75 %	m	11 %
f	91 %	f	13 %
m+f	84 %	m+f	12 %

Table 43. Survival during the tenth and eleventh years after fledging.

Year Fledged	Sex	n10	s10	d10	e10	p10
1982	m	3.00	2.00	1.00	0.86	0.67
	f	3.00	3.00	0.00	0.86	1.00
1983	m	0.00	0.00	0.00	0.00	0.00
	f	1.00	0.00	1.00	0.29	0.00

Total		N10	S10	D10		P10
	m	3.00	2.00	1.00		0.67
	f	4.00	3.00	1.00		0.75
	m+f	7.00	5.00	2.00		0.71

Survival (S10/N10*100)		Survival from fledging (P1*P2*..P10*100)	
m	67 %	m	7 %
f	75 %	f	10 %
m+f	71 %	m+f	9 %

Year Fledged	Sex	n11	s11	d11	e11	p11
1982	m	2.00	1.00	1.00	0.80	0.50
	f	3.00	2.00	1.00	1.20	0.67

Total		N11	S11	D11		P11
	m	2.00	1.00	1.00		0.50
	f	3.00	2.00	1.00		0.67
	m+f	5.00	3.00	2.00		0.60

Survival (S11/N11*100)		Survival from fledging (P1*P2*..P11*100)	
m	50 %	m	4 %
f	67 %	f	6 %
m+f	60 %	m+f	5 %

The lack of independence in the survival data between age classes prevented a comparison of survival between the sexes across all age classes, that was the first to the eleventh year. There were, however, sufficient data (the majority of expected frequencies exceeded 5.0) to compare male and female survival within the age classes one to six years (Table 44) from the data in Tables 35 to 40.

Table 44. Comparison of survival between sexes within age classes.

Age class	Chi-squared with df = 1	p
1st	0.000	>0.05
2nd	0.011	>0.05
3rd	0.803	>0.05
4th	0.060	>0.05
5th	0.369	>0.05
6th	0.613	>0.05

There was no significant difference in survival between males and females within the first six age classes (Table 44).

Survival data for both sexes were, therefore, combined in order to investigate year effect within age classes. There were sufficient data for this analysis to be undertaken (Table 45) on only the first, second and third age classes in Tables 35, 36 and 37.

Table 45. Comparison of survival between years within age classes one, two and three.

Age class	Chi-squared	df	p
1st	14.233	10	>0.05
2nd	18.871	9	<0.05
3rd	12.622	8	>0.05

Survival was significantly lower amongst birds in the second age class (Table 45) which fledged in 1991 (Table 36) and were in their second year during the period 1992-1993. Survival was low also amongst birds which fledged in 1983 and were in their second year during the period 1984-85, however, data were rather few for that cohort.
There were periods of very cold and wet weather, together with strong winds, during the winter of 1992-93 (Elkins 1993; Elkins 1994). While a proportion of first year birds may have remained with their parents during that winter and thereby benefited from their experience in surviving during adverse conditions, swans in their second year would have been independent of their parents and possibly been less able, due to a lack of experience, to endure such conditions. Birds in their third year may have benefited from their longer experience of life in order to cope with winter conditions.

Since there was evidence of a year effect it followed that the non-homogeneous data should have been excluded from any compilation of data within age classes and across years. In practice this would have resulted in another source of error since it was possible to test for homogeneity in only the first three data sets. Consequently survival data for the year which exhibited a year effect were not excluded from the totals in Table 36; it is acknowledged that this may have caused an inaccuracy in the survival estimates for that age class and in the estimated rates of survival from fledging. This difficulty can only be overcome through an increase in the number of data in age classes four to eleven years which will involve monitoring survival of the 1992 cohort for at least eleven years, until the year 2003.

Estimated survival rates (Figure 26) show survival was lower in the first year after fledging than in the subsequent eight years for both males and females. There was an indication that survival decreased in the tenth and eleventh years.

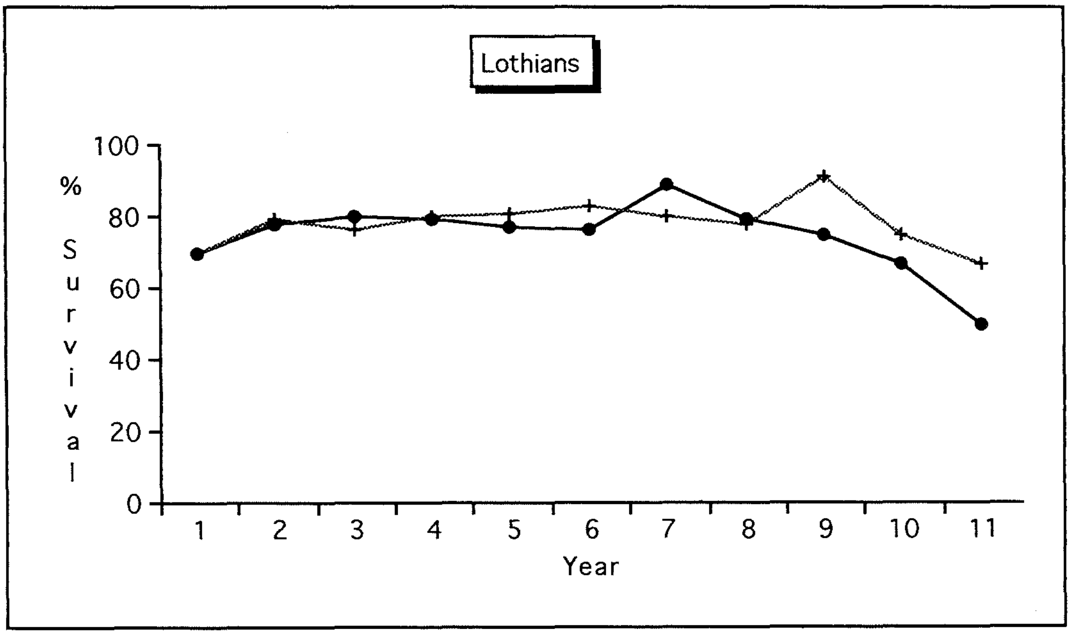


Figure 26. The percentage of Lothians male (●) and female (+) swans which survived each year after fledging.

The number of data in the tenth and eleventh age classes were few. Combining data from both sexes for the last two age classes (Figure 27) suggested the downward trend was real. Continuation of the study is the only way to substantiate this apparent trend which may be indicative of a terminal decline in Mute Swan survival.

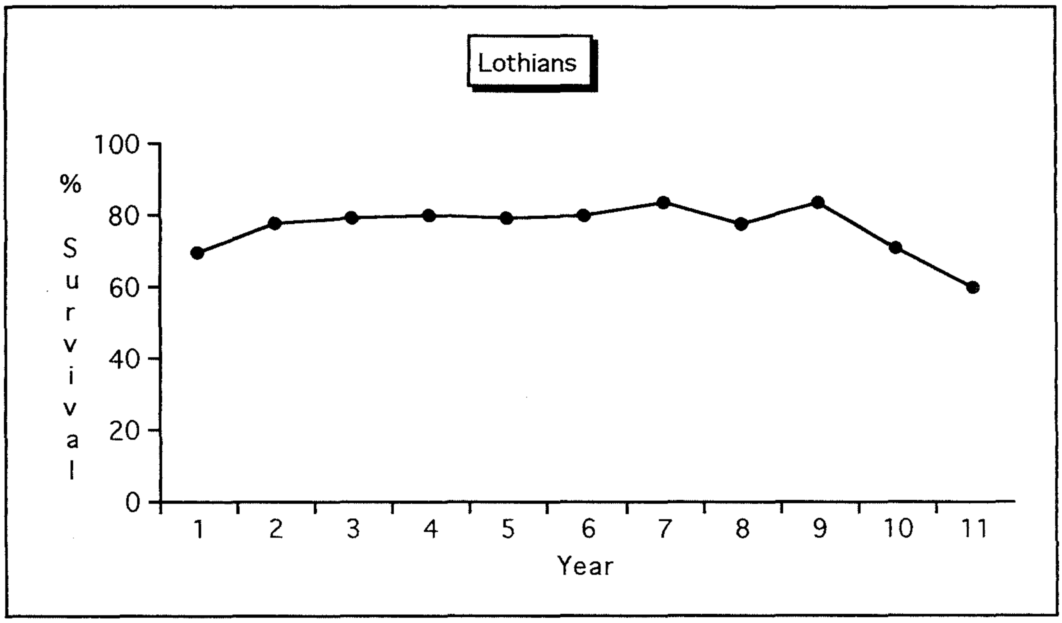


Figure 27. The proportion of Lothians swans which survived each year after fledging, sexes combined.

Results from other British studies

Details of the data in Table 46 are as follows -

- Estimated survival for the Lothians from Tables 35 to 43.

- Survival of Abbotsbury cygnets ringed in September, from 1970 to 1979, to September in the following year and in subsequent years from September to the following September. Data from Perrins and Ogilvie (1981) and based on 535 ringed cygnets.

- Survival of South Staffordshire (1) hatched cygnets from fledging in August to the following August and in subsequent years from August to the following August. Data from Coleman and Minton (1980) and based on 1375 cygnets fledged and ringed from 1961 to 1977.

- Survival of South Staffordshire (2) hatched cygnets from fledging in August to the following August and in subsequent years from August to the following August. Data from Coleman et al. (1991) and based on 2157 cygnets fledged and ringed from 1961 to 1985, thus they include the previous data set.

- Survival of cygnets, ringed in the Oxford Area between 1960 and 1966, from October in year of hatching to the following March and annually from 1st April to following 31st March. Data from Perrins and Reynolds (1967).

- Survival of cygnets, ringed in the Hebrides between 1978 and 1982. Data from Birkhead and Perrins (1986).

- Survival of cygnets, in the Wylye Valley and ringed during the period July to September, from ringing to the following August and in subsequent years from August to the following August. Data from Trump et al. (1994) and based on 499 birds hatched between 1974 and 1987.

Table 46. Annual survival rates for Mute Swans in six areas of Britain.

	Annual survival (%)						
Age class	Lothians	Abbotsbury	Stafford 1	Stafford 2	Oxford	Hebrides	Wylye
1	70	68	44	43	77	58	63
2	78	91	68	68	63	75	70
3	79	89	69	65	69	76	68
4	80	93	77	73	69	75	74
5	79	87	80	75			
6	80	90					
7	84	81					
8	78	83					
9	84	88					
10	71						
11	60						

The patterns of survival determined for the Abbotsbury, South Staffordshire, Hebrides and the Wylye Valley studies were consistent with the pattern in the Lothians study

where survival in the first year was lower than in subsequent years (Table 46). In contrast, survival in the Oxford study was greater in the first year than in subsequent years. The apparently abnormal pattern demonstrated by the Oxford population probably resulted form particularly high mortality following the exceptionally severe winters of 1961-62 and 1963-64 (Perrins and Reynolds 1967).
Although first year survival in the Oxford study appeared to be comparatively high, the data represent survival for just a six month period from October to March. This period was not consistent with the eight month period covered by the Lothians data; South Staffordshire and Abbotsbury results covered twelve month periods. The proportion of deaths would inevitably be lower in a shorter time period and hence direct comparison of the Oxford results with those for the other studies was inappropriate. Similarly, direct comparisons of the Lothian first year results with those for Abbotsbury, South Staffordshire, Hebrides and the Wylye Valley would be misleading.

Perrins (1991b) analysed the ringing and recovery data held by the British Trust for Ornithology up to 1988 and found mortality to be particularly high during the first few months post-fledging when many young birds took their maiden flight and had to fend for themselves.

Perrins and Sears (1991) found that mortality was not constant throughout the year and also varied between age classes. A proportional adjustment, for instance to first age class survival rates given in Table 46, in order to make them comparable with the eight month period for the

Lothians could not be justified since it would have resulted in incorrect survival rates. Consequently it was not possible to conclude whether survival in the Lothians was high or low relative to survival in other areas of Britain.

Survival from fledging

The majority of swans in Britain were believed to commence breeding about the age of three years. The proportions of birds which survived from fledging to breeding age in the Oxford and South Staffordshire studies (Figure 28) were low and suggested the size of those populations might be declining. While the South Staffordshire population was, in fact, in decline, the Oxford population was not; the pattern of survival in the Oxford area shown in Figure 28 was undoubtedly a consequence of the severe weather of the 1961-62 and 1963-64 winters. This highlighted the value of long-term monitoring in order to identify a year effect on survival for long-lived species.

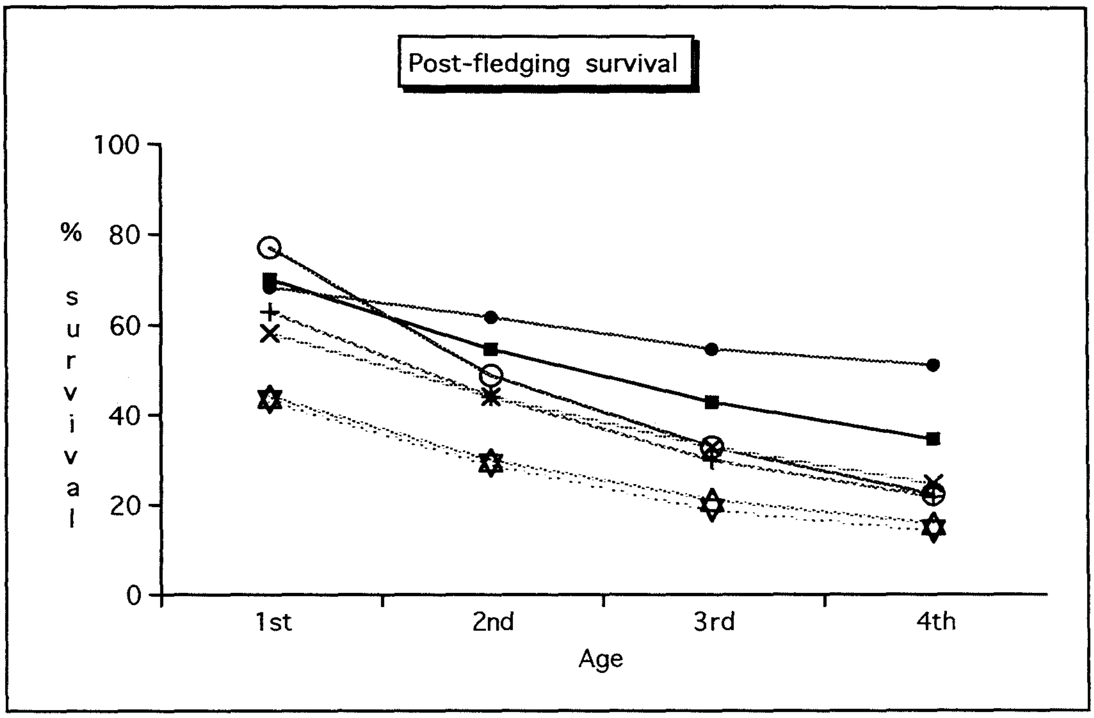


Figure 28. Survival from fledging at Oxford (o), Lothians (■), Abbotsbury (●), Wylye (+), Hebrides (x), South Staffordshire 1 (△) and South Staffordshire 2(▽) in the first four years post-fledging.

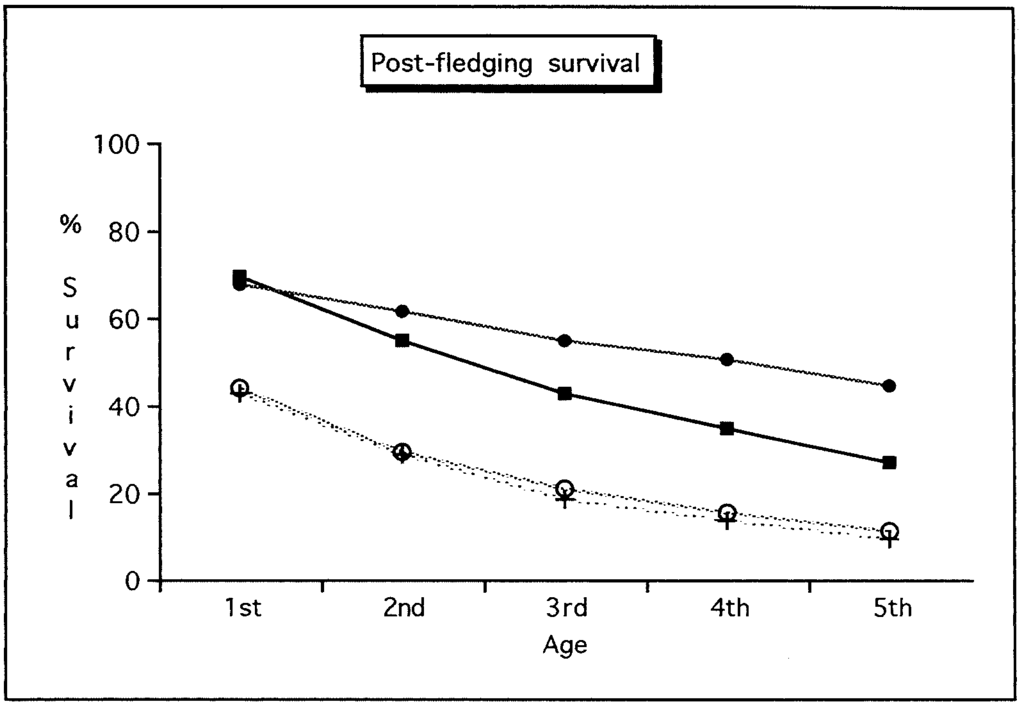


Figure 29. Survival from fledging at Abbotsbury (●), Lothians (■), South Staffordshire 1 (o) and South Staffordshire 2 (+) in the first five years post-fledging.

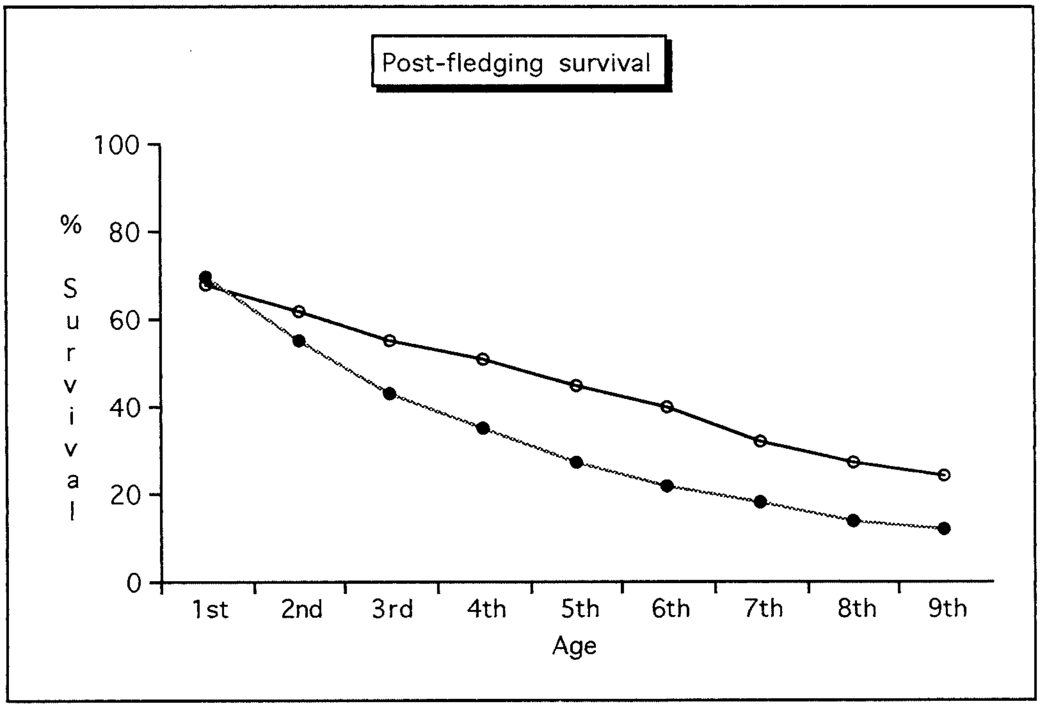


Figure 30. Survival from fledging at Abbotsbury (o) and in the Lothians (●).

It was apparent from Figure 29 that only a small proportion of South Staffordshire birds survived beyond the age of five years and it seemed probable that the breeding population would be comprised primarily of birds aged three to five years.
With over 10% of the Lothians and Abbotsbury populations surviving to the ninth year after fledging (Figure 30) it was probable that the age range and structure of the breeding population in those areas differed from those for South Staffordshire. It follows that age-specific proportions of birds breeding for the first time would be expected to vary between study areas.

Over 25% of fledged birds survived to at least their fifth year in the Lothians and Abbotsbury. The greatest survival rates appeared to occur in the Abbotsbury population (Figure 30) and probably reflected its geographical location in south west Britain where winter weather is generally milder than in eastern Scotland.

Age specific number of cygnets fledged per breeding pair

The estimated survival rates for Lothians males and females (Tables 35 to 43) were applied to the number of cygnets fledged per breeding pair (Chapter 5, Table 27) in order to estimate the number of cygnets fledged per breeding pair which survived to each age class (Tables 47, 48 and 49).

Table 47. The estimated number of <u>male</u> Mute Swans produced per breeding pair which survived to the age of 11 years.

Age from fledging	Survival from fledging	Combined habitats	Canal	River	Still water	Still water 0-50m
Flg		1.40	1.76	1.04	1.45	1.10
1	0.70	0.98	1.24	0.73	1.02	0.77
2	0.55	0.77	0.97	0.57	0.80	0.61
3	0.44	0.62	0.78	0.46	0.64	0.48
4	0.35	0.49	0.62	0.36	0.51	0.38
5	0.27	0.38	0.48	0.28	0.39	0.30
6	0.20	0.28	0.35	0.21	0.29	0.22
7	0.18	0.25	0.32	0.19	0.26	0.20
8	0.14	0.20	0.25	0.15	0.20	0.15
9	0.11	0.15	0.19	0.11	0.16	0.12
10	0.07	0.10	0.12	0.07	0.10	0.08
11	0.04	0.06	0.07	0.04	0.06	0.04

Table 48. The estimated number of <u>female</u> Mute Swans produced per breeding pair which survived to the age of 11 years.

Age from fledging	Survival from fledging	Combined habitats	Canal	River	Still water	Still water 0-50m
Flg		1.30	1.64	0.96	1.35	1.00
1	0.70	0.91	1.14	0.67	0.94	0.70
2	0.55	0.71	0.90	0.53	0.74	0.55
3	0.42	0.55	0.69	0.40	0.57	0.42
4	0.34	0.44	0.56	0.33	0.46	0.34
5	0.27	0.35	0.44	0.26	0.36	0.27
6	0.23	0.30	0.38	0.22	0.31	0.23
7	0.18	0.23	0.29	0.17	0.24	0.18
8	0.14	0.18	0.23	0.13	0.19	0.14
9	0.13	0.17	0.21	0.13	0.18	0.13
10	0.10	0.13	0.16	0.10	0.13	0.10
11	0.06	0.08	0.10	0.06	0.08	0.06

Table 49. The estimated number of Mute Swans produced per breeding pair which survived to the age of 11 years.

Age from fledging	Survival from fledging	Combined habitats	Canal	River	Still water	Still water 0-50m
Flg		2.70	3.40	2.00	2.80	2.10
1	0.70	1.89	2.38	1.40	1.96	1.47
2	0.55	1.49	1.87	1.10	1.54	1.15
3	0.43	1.16	1.46	0.86	1.20	0.90
4	0.35	0.94	1.19	0.70	0.98	0.73
5	0.27	0.73	0.92	0.54	0.76	0.57
6	0.22	0.59	0.75	0.44	0.62	0.46
7	0.18	0.49	0.61	0.36	0.50	0.38
8	0.14	0.38	0.48	0.28	0.39	0.29
9	0.12	0.32	0.41	0.24	0.34	0.25
10	0.09	0.24	0.31	0.18	0.25	0.19
11	0.05	0.14	0.17	0.10	0.14	0.10

The age range of swans which bred for the first time is determined in Chapter 7. This information, in conjunction with the data in Tables 47, 48 and 49, also enabled the estimation of the age-specific number of cygnets fledged per breeding pair in the Lothians which survived to breeding age (Figure 1) in Chapter 7.

Discussion

Few publications were traced regarding the sex ratio in waterfowl at hatching. Swennen et al. (1979) reported an equal sex ratio at hatching in the Common Eider *Somateria mollissima* (L) in the Dutch Waddenzee and also found that by the time of fledging there were significantly more males

(54.2%) than females due to differential mortality between hatching and fledging. Mathiasson (1981b) found the proportions of males and females were similar and, since there was no difference in mortality rates between both sexes, the proportions were similar at fledging.
Mute Swan cygnets were sexed at hatching at Abbotsbury in 1991 and 1995 (Chris Perrins, pers. comm.). The cygnets in 1991 comprised 266 males, 208 females and although some complete broods were not sexed only 9 cygnets from broods where their siblings were sexed evaded examination. Even if all 9 'odd' cygnets were females there were significantly more males than females (Chi-squared = 4.971, df 1, $p<0.05$). There was no difference in the proportion of males and females in 1995 with 98 males and 94 females and only 2 birds not sexed. A significant bias in favour of males was thus recorded at hatching at Abbotsbury in 1991 but not in 1995. These birds were not re-examined at fledging and, therefore, differential mortality between males and females prior to fledging was not established.

The disparity in favour of male swans, recorded in some studies at the fledging stage, may have been present at hatching or, if the number of males and females was equal at hatching, the disparity could have arisen as a result of differential mortality between hatching and fledging. The sex ratio at the small young stage was not investigated in the present study and there was a lack of conclusive information from elsewhere to justify any assumption regarding the sex ratio in Lothians swans at the time of hatching, nor during the small, medium and large size stages in cygnet growth. Consequently, it was necessary in Chapter 8, to base calculations of the intrinsic proportions of males and females breeding in the Lothians on the number of male and female cygnets fledged per breeding pair. Ideally, in studies of bird populations, such calculation should be based on the number of male and female cygnets at birth i.e. the number hatched per breeding pair, or the number of male and female eggs laid.

The variations in criteria for ageing swans adopted by various studies should be borne in mind in any attempt to compare survival rates between populations in specific age classes. In addition, the variations prevented a conclusion being reached regarding the relative status of survival rates estimated for the Lothians population. There is an obvious need for a standardised system for the ageing of Mute Swans in order to facilitate meaningful comparisons of results between populations.

Although the principal cause of death amongst swans in Britain was identified as flying accidents (Ogilvie 1967; Perrins and Sears 1991; Brown et al.1992) there were regional variations. Lead poisoning was a major cause of mortality in the Warwickshire area (Hardman and Cooper 1980) and on the River Thames (Birkhead 1982) whilst collision with overhead cables was prevalent in the South Staffordshire area (Coleman et al. 1991). In the Outer Hebrides collision with overhead cables was cited also as the principal cause of mortality (Spray 1991). Many of these studies reported finding casualties close to the natal site and suggested the high mortality rate in the first year of life occurred during the first few flights post-fledging; this was probably the case in the Lothians. McDonald et al. (1987) reported the findings of 67 Mute

Swan post mortem examinations carried out between 1980 and 1984. Within that group 29 were collected in the Tyninghame area of East Lothian and 26 were recovered in the Montrose Basin area; the most common cause of death among those birds was lead poisoning. Both sites were subject to wildfowling and it was presumed the birds died as a result of ingesting spent lead shot.

Post mortem examinations, undertaken between 1986 and 1990 at the M.A.F.F. Lasswade Veterinary Laboratory, Bush Estate, Penicuik or the D.A.F.S. Wildlife Incident Service, East Craigs, Edinburgh, on 19 Mute swans found dead in the Lothians, were made available by the people who submitted corpses for analyses. Results of those analyses (7 male, 9 female, 3 unknown sex) revealed that in 6 cases the cause of death was unknown, 5 died from disease, 4 from lead poisoning, 1 from gorging grain, 1 from trauma (found beneath cables), 1 from fishing tackle and 1 shot.

In the study area many swans were known to have collided with overhead cables (J. McGregor and J. Helliwell pers.comm.), collided with buildings or even found impaled on railings and reports were received of swans having collided with trains and other vehicles. The relatively constant survival rate from years two to nine was consistent with the random nature of such incidents in the Lothians. Following many of those incidents the cause of death was either apparent or the carcass was irretrievable, and post mortem examination was not undertaken.

Consequently the 19 birds which were analysed did not constitute a sufficiently representative sample from the study area to enable a quantitative assessment of causes of mortality in Lothians Mute Swans to be made.

Analyses of 164 blood samples taken from live adults and broods in the study area between 1983 and 1985 indicated that 40% of 1983 samples, 6% of 1984 samples and 62% of 1985 samples gave elevated blood lead levels, where concentrations in excess of 40μg/100ml^{-1} were considered to be elevated (Spray and Milne 1988). Ranges were 20-67μg/100ml^{-1} in 1983, 19-60μg/100ml^{-1} in 1984 and 9-1370μg/100ml^{-1} in 1985. The authors suggested this was a pattern of sporadic cases of high blood-lead levels, and that lead poisoning in Mute Swans was less important in Scotland than in England.

Factors contributing to deaths of Mute Swans in Lothians, therefore included collision with objects and lead poisoning, in addition to a variety of other factors such as disease, entanglement in and ingestion of fishing tackle and being shot.

Chapter 7

The Breeding Population

Introduction

Perrins and Reynolds (1967) determined the age of Mute Swans at first breeding in the Oxford area during the period from 1960 to 1966. Additionally, they calculated post-fledging mortality rates in birds hatched in their study area and the level of mortality in the breeding population. From this information they constructed a life table and concluded that productivity was sufficient to balance mortality in the adult population.

At about the same time, Minton (1968) found the age at first breeding in the South Staffordshire population to be similar to that in the Oxfordshire area. He was able also to determine mean mortality in the South Staffordshire breeding population, though he did not devise a life table.

During the subsequent period of almost 25 years, there have been two further investigations in Britain into the ability of a Mute Swan population to maintain its numbers. Perrins and Ogilvie (1981) found that between 1969 and 1980 the Abbotsbury population was able to sustain its numbers by its own productivity and Trump et al. (1994) came to a similar conclusion with regard to the population in the Wylye Valley between 1978 and 1993.

Results from other studies have included estimates of the balance in the number of swans in populations by combining Perrins and Reynolds' 1960's post-fledging data with pre-fledging data from their own shorter studies, for example Bacon (1980) and Birkhead and Perrins (1985). The inaccuracies resulting from such an approach were acknowledged by the authors.

Birkhead and Perrins (1986), Perrins (1991a) and Bacon and Perrins (1991) lacked additional sources of data in order to describe the demographic features of Mute Swan populations in Britain. Clearly there was a requirement for more precise investigation of population dynamics based on more recent data.

Results

Age structure of the breeding population

Although colour ringing in the Lothians commenced in 1982, there were too few data to illustrate the age structure of the breeding population for the years prior to 1990. Figures 31 to 34 illustrate the age structure in each of the years from 1990 to 1993 and indicate that even by 1993 there was no consistent pattern. A stable pattern could be expected to emerge once the study had run long enough to cover the maximum life span of breeding swans in the study area. The lifespan in the Lothians appeared to be at least sixteen years. This was determined from the few swans which were ringed as cygnets in the Lothians prior to commencement of the present study and were recorded breeding during the present study. A male (AXN) aged fourteen years when it bred in 1993, also bred in 1994 and 1995 while a female (080/CAI/HLU) aged eleven years when it bred in 1993, also bred in 1994 but died early in 1995. The age of swans which bred in the Lothians during the study ranged from 2 to 14 years for males and 2 to 13 years for females.

A breeding population which increased in numbers and demonstrated low mortality in combination with high productivity might have shown an increase in its mean age at first breeding; the converse might occur in a declining breeding population. Such movement in the mean age would probably be gradual and would require a number of years of continuous monitoring in order to be detected.

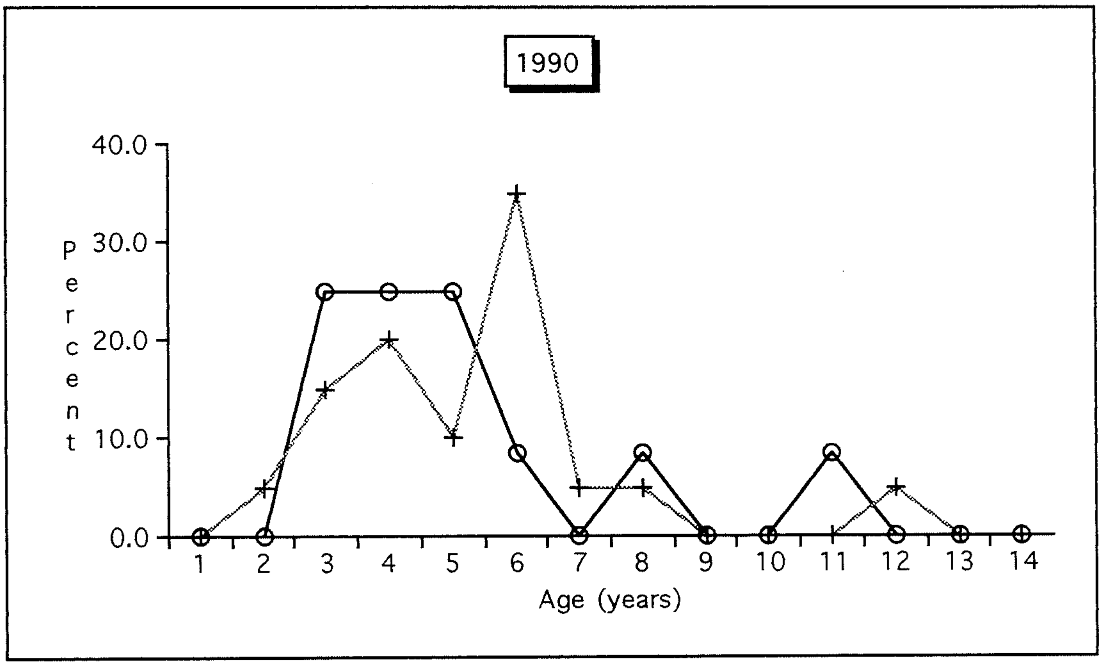


Figure 31. Age structure of the breeding population in 1990, males (o) (n = 12) and females (+) (n = 20).

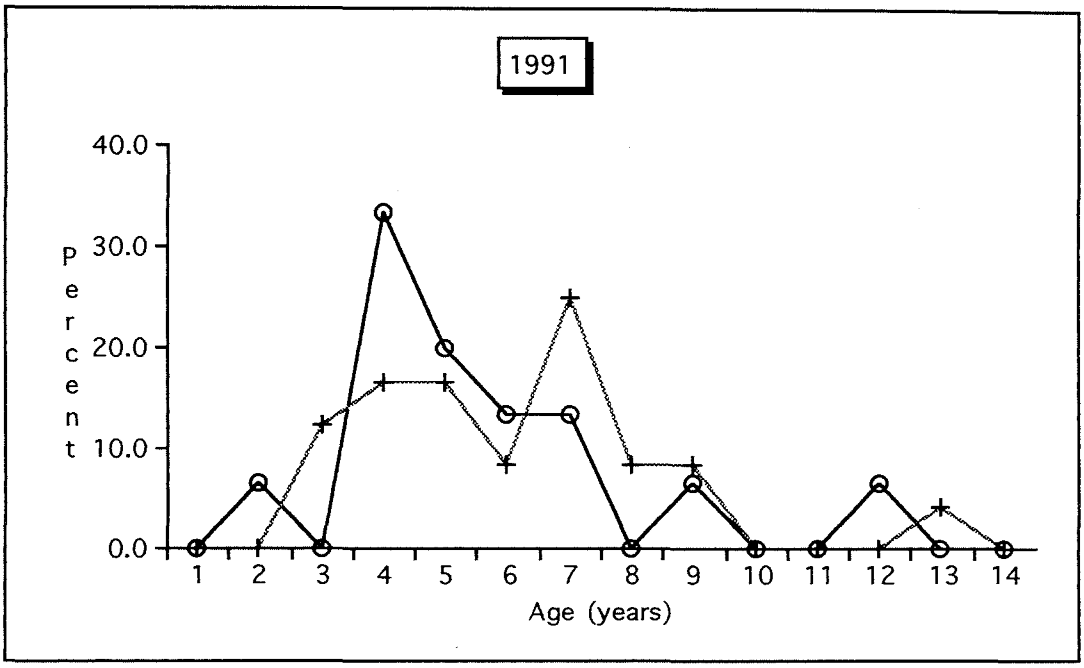


Figure 32. Age structure of the breeding population in 1991, males (o) (n = 15) and females (+) (n = 24).

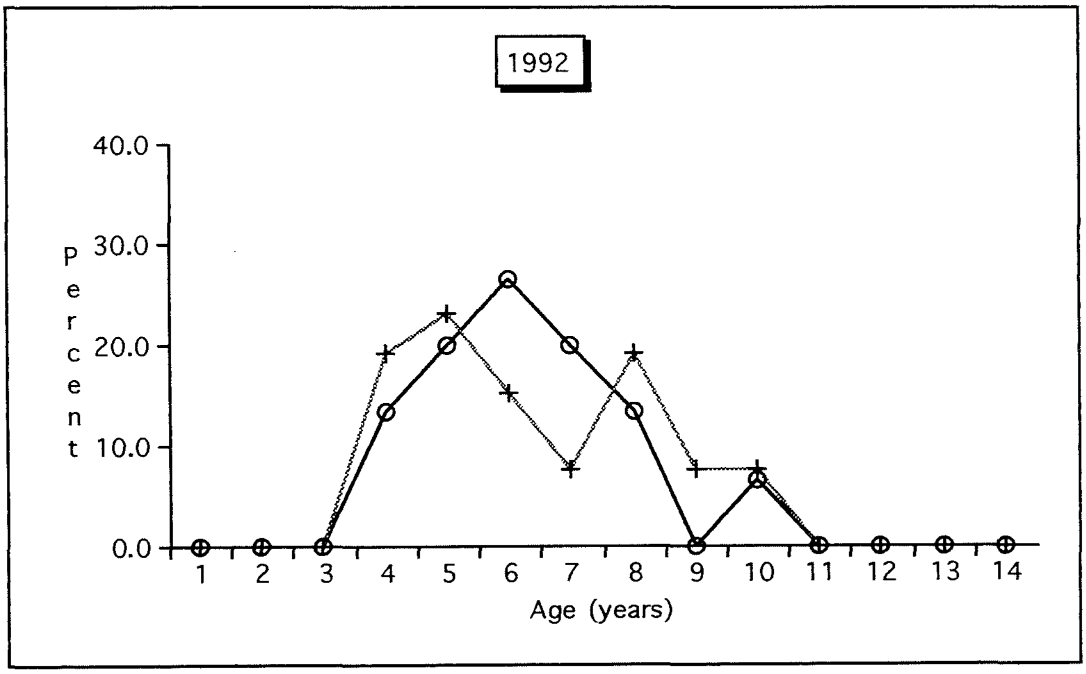


Figure 33. Age structure of the breeding population in 1992, males (o) (n = 15) and females (+) (n = 26).

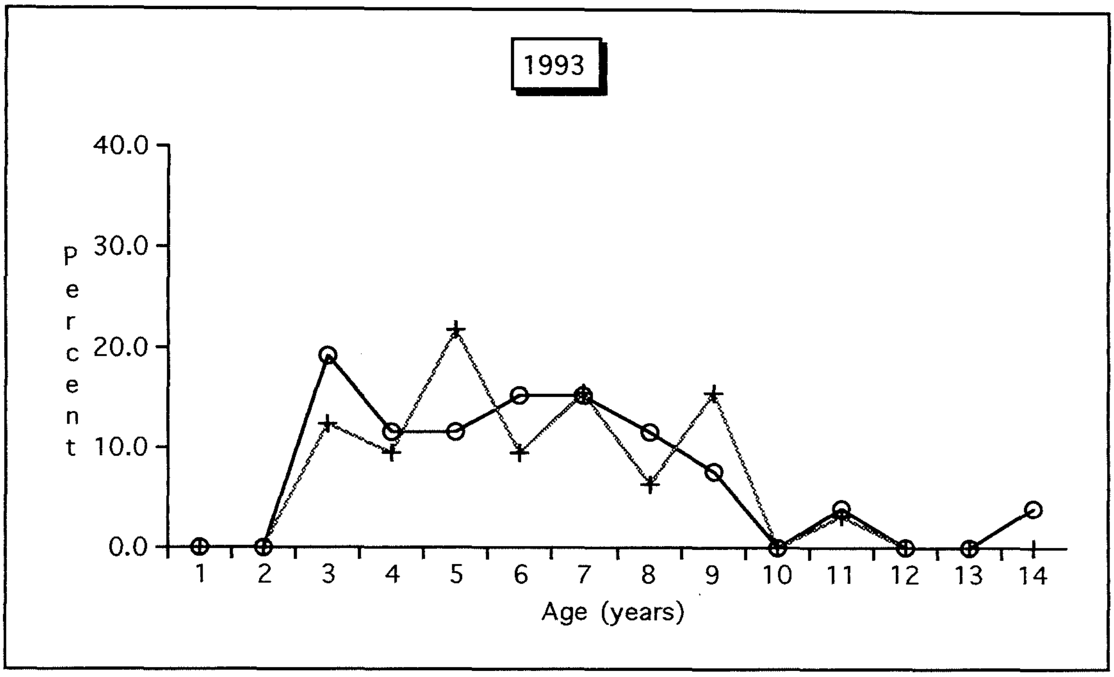


Figure 34. Age structure of the breeding population in 1993, males (o) (n = 26) and females (+) (n = 32).

Age at first breeding

From the data collected during the period 1982 to 1993 the age at first breeding was determined for 26 males and 40 females (Table 50). Although 40% of females bred for the first time at or over the age of five years compared with 19.1% of males, the mean age at first breeding for females (4.3 years) was not significantly different from that for males (3.7 years) ($z = 1.66$, $p>0.05$). Inclusion of data on immigrants, 4 males and 3 females, made little difference to the outcome with the female mean slightly reduced to 4.2 years and male mean increased to 3.8 years.

Table 50. Age at first breeding in the Lothians population.

Age/years	1	2	3	4	5	6	7	8-11
% Males	0	3.8	50.0	26.9	11.5	3.8	3.8	0
% Females	0	2.5	32.5	25.0	20.0	12.5	7.5	0
% Sexes combined	0	3.0	39.4	25.7	16.7	9.1	6.0	0

No swan bred for the first time in the Lothians at the age of 1 year and no swan bred for the first time over the age of 7 years (Table 50). Since colour ringing commenced in 1982, it was feasible for birds in the age range of 8 to 11 years to have been recorded breeding for the first time by 1993; therefore, the age range at first breeding was not truncated by the length of the study period.

Results from other studies

Variation in the criteria adopted for ageing swans in different areas precluded a statistical comparison of results in Table 51. Since the criteria were not detailed in all those studies it was not possible to adjust the data in order to facilitate direct comparison. From the information which was available it was concluded that the mean age at first breeding in the Lothians was greater than in the Oxford area but probably lower than in most of the remaining studies listed in Table 51.

The age ranges in the Oxford, South Staffordshire and Northumberland populations were fairly narrow and may have been truncated by the short time scale of those studies.

Table 51. Mean age at first breeding; a comparison with other studies.

Study Area	Mean age at first breeding in years (range)	Study period	Data source
Northumberland	3.7 (2-5)	1989-1993	J. Coleman pers.comm.
Oxford	3.6 (2-6)	1960-1966	Perrins and Reynolds 1967
South Staffordshire	3.7 (2-6)	1961-1967	Minton 1968
Wylye Valley	4.5	1978-1993	Trump et al. 1994
Abbotsbury (Radipole Lake)	4.8 (3-10)	1969-1980	Perrins and Ogilvie 1981
Copenhagen, Denmark	5.0 (4-8+)	1967-1975	Andersen-Harild 1981.
Lothians	4.1 (2-7)	1982-1993	Present study

Table 52. Age at first breeding for males and females.

Study Area	Mean age at first breeding (years)	
	Males	Females
Oxford	3.8	3.4
South Staffordshire	3.8	3.6
Abbotsbury (Radipole Lake)	4.9	4.7
Copenhagen, (Denmark)	5.0	4.7
Lothians	3.7	4.3

In contrast to the findings of some studies the mean age at first breeding was slightly lower for males than females in the Lothians (Table 52), however, the difference between the mean ages for males and females in the Lothians was not significant (p163).

A population of colonial breeding swans developed at Roskilde, Denmark after 1975. The age at first breeding for males and females in the colonial breeding Roskilde and non-colonial Kobenhavn populations are listed in Table 53.

Table 53. Age at first breeding for males and females in the Danish study, from Bacon and Andersen-Harild (1989).

Sub-population	Mean age at first breeding (years)	
	Males	Females
Roskilde, 1972-86	5.9	5.3
Kobenhavn, 1966-1986	5.9	6.0
Kobenhavn, 1972-1986	5.4	5.8
Lothians	3.7	4.3

As in the Lothian population, it was apparent that females in the Kobenhavn population were breeding for the first time at a greater (not significantly greater) age than males. Therefore, a slightly greater mean age at first breeding among females than males may have been associated with slightly lower mortality among breeding females than males (Table 66).

Difference in the age of swans in a breeding pair

From the available data it was possible to determine the age of both the male and female in 24 breeding pairs. In the cases of 75% of these pairs there was no more than 1 year of difference in the ages of the birds (Table 54). A tendency was detected for a male to pair with a female older than himself; 37.6% of males paired with an older female and 25.0% paired with a female who was younger.

However, the mean age of males was not significantly different ($t = 0.277$, df 23, $p>0.1$) from the mean age of females in those breeding pairs.

Table 54. Age difference between birds in breeding pairs.

Age of male less age of female (years)	Number of Pairs	% of Pairs
+5	2	8.3
+4	1	4.2
+3	0	0
+2	1	4.2
+1	2	8.3
0	9	37.5
-1	7	29.2
-2	0	0
-3	1	4.2
-4	0	0
-5	1	4.2

There were three instances in which the age difference between birds in a breeding pair was known and in later years it was found that one bird from a pair later re-paired with another bird of known age; re-pairing generally followed the death of the original mate.

a). Male AZX was originally paired
with Female 735 age difference -3 yrs
Male AZX re-paired
with Female HXL age difference +4 yrs

b). Male CBI was originally paired
with Female AXS age difference -1 yr
Female AXS re-paired
with Male AXZ age difference 0 yrs

c). Male BNU was originally paired
with Female CSX age difference +1 yr
Male BNU re-paired
with Female AYS age difference +2 yrs

The two males which re-paired did so with a female younger than themselves and younger than their original mate while the female which re-paired did so with a male of the same age as herself and older than her original mate. There was, therefore, a tendency within these three pairs for males to pair with a younger female. The reason for this tendency is unclear.

Age-specific number of swans which survived to breeding age

Results show that Mute Swans in the Lothians study area commenced breeding between the ages of 2 and 7 years. The percentage of males (n = 26) and females (n = 40) which bred for the first time in each age class (Table 50) was applied to the number of cygnets produced per breeding pair for combined habitats and individual habitats (Chapter 6, Tables 47 and 48) in order to determine the number of cygnets a breeding pair might have contributed annually to the breeding population (Tables 55 to 64).

Table 55. Males, habitats combined.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	3.8	0.77	0.029
3	50.0	0.62	0.310
4	26.9	0.49	0.132
5	11.5	0.38	0.044
6	3.8	0.28	0.011
7	3.8	0.25	0.009
Total			0.535

Table 56. Females, habitats combined.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	2.5	0.71	0.018
3	32.5	0.55	0.179
4	25.0	0.44	0.110
5	20.0	0.35	0.070
6	12.5	0.30	0.038
7	7.5	0.23	0.017
Total			0.431

Table 57. Males on canals.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	3.8	0.97	0.037
3	50.0	0.78	0.390
4	26.9	0.62	0.167
5	11.5	0.48	0.055
6	3.8	0.35	0.013
7	3.8	0.32	0.012
Total			0.674

Table 58. Females on canals.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	2.5	0.90	0.023
3	32.5	0.69	0.224
4	25.0	0.56	0.140
5	20.0	0.44	0.088
6	12.5	0.38	0.047
7	7.5	0.29	0.022
Total			0.544

Table 59. Males on rivers.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	3.8	0.57	0.022
3	50.0	0.46	0.230
4	26.9	0.36	0.097
5	11.5	0.28	0.032
6	3.8	0.21	0.008
7	3.8	0.19	0.007
Total			0.396

Table 60. Females on rivers.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	2.5	0.53	0.013
3	32.5	0.40	0.130
4	25.0	0.33	0.083
5	20.0	0.26	0.052
6	12.5	0.22	0.027
7	7.5	0.17	0.013
Total			0.318

Table 61. Males on still waters.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	3.8	0.80	0.030
3	50.0	0.64	0.320
4	26.9	0.51	0.137
5	11.5	0.39	0.045
6	3.8	0.29	0.011
7	3.8	0.26	0.010
Total			0.553

Table 62. Females on still waters.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	2.5	0.74	0.019
3	32.5	0.57	0.185
4	25.0	0.46	0.115
5	20.0	0.36	0.072
6	12.5	0.31	0.039
7	7.5	0.24	0.018
Total			0.448

Table 63. Males on still waters 0 - 50 m.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	3.8	0.61	0.023
3	50.0	0.48	0.240
4	26.9	0.38	0.102
5	11.5	0.30	0.035
6	3.8	0.22	0.008
7	3.8	0.20	0.008
Total			0.416

Table 64. Females on still waters 0 - 50 m.

Age (years)	% Breeding for the first time	No. cygnets produced per breeding pair which survived to age class	No. cygnets produced per breeding pair which could have bred
2	2.5	0.55	0.014
3	32.5	0.42	0.136
4	25.0	0.34	0.085
5	20.0	0.27	0.054
6	12.5	0.23	0.029
7	7.5	0.18	0.014
Total			0.332

The total number of cygnets produced per breeding pair which could have bred and calculated in Tables 55 to 64 are summarised in Table 65 in order to facilitate their frequent use in Chapter 8. The greater productivity values for males than females in Table 65 reflect the slightly greater proportion of males than females at fledging (although not significant) and the similarity in male and female post-fledging survival rates, while the differences between habitats reflects the variation in pre-fledging survival rates between the habitats.

Table 65. Summary of productivity per breeding pair per annum to the age of first breeding (range 2 to 7 years).

Breeding habitat	Males	Females
Canals	0.67	0.54
Rivers	0.40	0.32
Still Waters	0.55	0.45
Still Waters 0-50m	0.42	0.33
Combined Habitats	0.53	0.43

A lack of data regarding the age specific proportion of swans which bred for the first time has resulted in a number of biologists working on swans basing their estimates of the number of cygnets produced per breeding pair which survived to breed on the number of cygnets which survived to the mean age of first breeding (Birkhead and Perrins 1986). Their results were potentially inaccurate

(Perrins 1991a) but the best available.

The number of cygnets produced per breeding pair which survived to the mean age of first breeding of four years in the Lothians was 0.49 males and 0.44 females (Chapter 6, Tables 47 and 48). Comparison with the finding for combined habitats in Table 65 (0.54 males and 0.43 females) indicated the use of a mean age of first breeding tended to under-estimate the number of males and over-estimate the number of females. Combination of results for both sexes suggested an overall under-estimate of 4%.

Mortality in the breeding population

Annual mortality in the breeding population was calculated from the number of ringed breeding birds at 1st April each year and the number of these birds which were dead by the following 31st March (Table 66).

Table 66. Annual mortality in the breeding population.

	Males		Females	
Year	No. Deaths	% Mortality	No. Deaths	% Mortality
1982	0	0	0	0
1983	1	16.7	2	22.2
1984	3	21.4	1	8.3
1985	5	31.2	2	13.3
1986	3	15.0	4	21.1
1987	4	17.4	3	15.0
1988	3	11.5	5	23.8
1989	4	14.8	2	8.0
1990	4	11.8	3	8.6
1991	3	7.9	6	13.5
1992	9	20.9	5	12.2
Total	39		33	
Mean		15.1%		13.5%

The wide range in the annual percentage of mortality was probably due to the low number of deaths in each year. Trump et al. (1994) estimated that mortality in the Wylye Valley breeding population covered a wide range also, from 3.4% to 22.0%, with a mean of 12.9%.

Mean annual mortality in the Lothians breeding population was 14.3% and the proportion of male deaths was not significantly different to the proportion of female deaths (Chi-squared = 0.26, df 1, $p>0.05$). Annual mortality per breeding pair was thus 0.15 male plus 0.13 female.

Mean mortality in the breeding population (14%, in age range 2 years and over) was less than in the general population (20%, in age range 2 years and over), a pattern also identified in the Abbotsbury population (Perrins and Ogilvie 1981). In contrast, mortality in both the solitary breeding and colonial breeding populations in Denmark was about 19% and greater than mortality in the general population of about 13% (Bacon and Andersen-Harild 1989). For some populations, the hazards incurred by breeding birds may not be as great as those incurred by non-breeding birds which were generally more mobile.

The number of birds which survived to breeding age, 0.53 males and 0.43 females per breeding pair (Table 65), exceeded the mortality figure of 0.15 males and 0.13 females per breeding pair. Therefore, male survival was 2.6 times and female survival 2.3 times in excess of that required to maintain a stable breeding population if immigration and emigration are disregarded at this stage.

Although productivity per breeding pair on river habitat was relatively low, the number of cygnets hatched on rivers and surviving to breeding age, 0.40 males and 0.32 females, also exceeded the mortality rate.

Age at death of ringed breeding swans

Data were rather few (Table 67) and in the older age groups birds were under-represented due to the length of the study. However, the mean age of breeding birds at death was 5 years for males and 7 years for females between 1982 and 1993 which suggested that breeding females survived longer than breeding males.

Table 67. The age (years) of dead ringed breeding birds.

Age at death	2	3	4	5	6	7	8	9	10	11	12	13	Total
No. Males	0	2	1	0	0	3	0	0	0	0	0	0	6
No. Females	0	1	0	3	3	2	0	0	1	0	0	1	11

The proportion of swans which bred at their natal site

A number of birds which hatched and were ringed in the study area were recorded breeding outside the study area. However, there was no consistent and systematic search for these birds and such records were inevitably biased towards birds breeding in areas frequented by ornithologists, therefore, data refer to birds which hatched and bred in the study area.

Data were available to calculate the distance between natal site and breeding site at the first breeding attempt for 26 males and 40 females. Females bred closer to natal site than males; there was a significant difference ($z = 2.58$, $p<0.05$) between the mean distance for males (12.8 km, range 0-60 km) and the mean distance for females (5.7 km, range 0-21.5 km). During the present study 42.3% of males bred within 5 km of their natal site compared with 57.5% of females, Figure 35.

The proportions of birds which bred for the first time at their natal site were 7.7% of males and 27.5% of females. Since these data were confined to birds which hatched and bred within the study area, and in the knowledge that some birds hatched in the Lothians were known to breed elsewhere, these were the maximum levels of philopatry for the Lothians population.

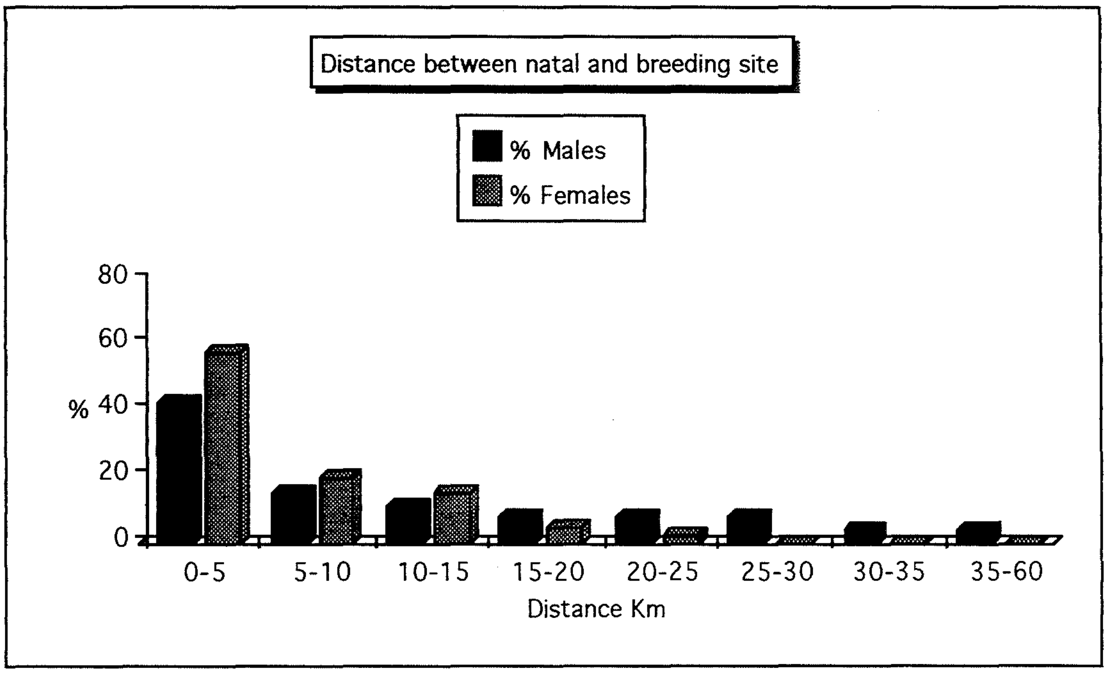


Figure 35. The distances male (n = 26) and female (n = 40) swans bred from their natal territory.

Data were available for 15 males and 26 females at their second breeding attempt. The data were fewer than for the first breeding attempt due to mortality or mate loss. One female moved into her natal site. Philopatry was 6.7% for males and 30.8% for females.

There was no philopatry among males at either the third (n = 9) or fourth (n = 7) breeding attempt, whereas the proportion for females at the third attempt was 26.3% (n =

19) and at the fourth attempt it was 26.7% (n = 15).

There was no significant difference between the mean age at first breeding for all females (4.3 years) and the mean age for philopatric females of 4.5 years, range 3-7 years ($t = 0.110$, df 49, $p>0.05$). Similarly there was no significant difference between the mean age at first breeding for all males (3.7 years) and the mean age for philopatric males of 3.5 years, range 3-4 years ($t = 0.295$, df 26, $p>0.05$).

Philopatric swans did not delay their first breeding attempt until they were able to occupy their natal site. In this respect, philopatry did not inhibit the number of life-time breeding attempts achieved by philopatric individuals.

Proximity of breeding pairs to natal territory

For 15 breeding pairs it was possible to determine the distance between natal and breeding site for both the male and female swan at their first attempt as a breeding pair (Figure 36). In 12 instances the pair bred closer to the female's natal site than the male's natal site; in seven of those cases the female bred in her natal site and the male bred in his natal site in two cases.

The mean distance of the females between natal site and breeding site (4.4 km) was significantly less ($t = 2.91$, df 14, $p<0.05$) than the mean for males (9.4 km) which confirmed that females bred closer to their natal site than males.

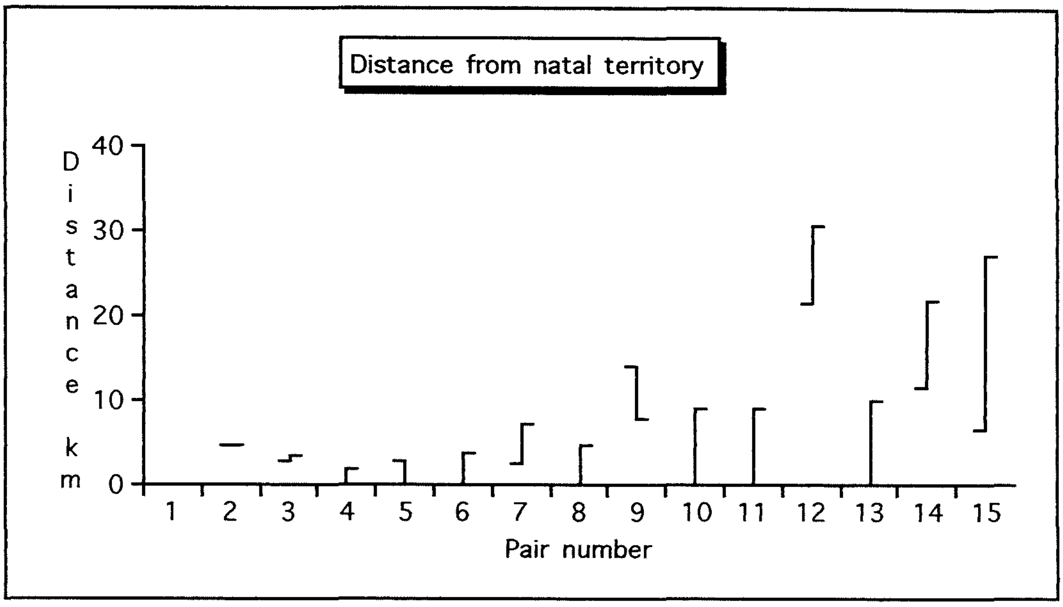


Figure 36. Distance of breeding territory from natal territory for the male ([) and female (]) in each of fifteen pairs.

The proportion of swans hatched in the Lothians which survived to breeding age and bred in the Lothians (Figure 1)

The maximum rate of philopatry among swans hatched in the Lothians was estimated above (pp.179-180). Although the actual rate of philopatry among birds hatched in the Lothians and which progressed to breed (inside and outside the Lothians) could not be calculated, it was possible to calculate the minimum rate of philopatry from the number of swans which hatched in the Lothians and survived to breeding age (as opposed to actually breeding), and the number of these birds which bred in their natal territory.

The age at which Mute Swans bred for the first time in the Lothians ranged from two to seven years (pp.163-4). The proportion of swans hatched in the Lothians which survived to breeding age and bred in the Lothians could, therefore, be calculated from the number of swans which hatched in the Lothians from 1982 to 1986; swans in the 1986 cohort could have survived to the age of seven years by 1993.

A. Number of cygnets fledged and ringed from 1982 to 1986 and survived to the age of two years (Table 36) was 122.

B. The percentages of swans which survived during each year from fledging were (Tables 37 to 41)

Year	3rd	4th	5th	6th	7th
% Survival	79	80	79	80	84

C. The numbers alive at the start of each age class were thus

Age class	2nd	3rd	4th	5th	6th	7th
No. alive at start of age class	122	96.4	77.1	60.9	48.7	40.9

D. The age specific percentages of swans which bred for the first time (Table 50) were

Age class	2nd	3rd	4th	5th	6th	7th
Percentage	3.0	39.4	25.7	16.7	9.1	6.0

and were applied to the above age specific number of swans alive at the start of each age class (C.) in order to calculate the number of swans which should have bred. Since the value was 78.7 but the number observed was infact 23 then it follows that 29.2% of swans which fledged in the

Lothians survived and bred in the Lothians; the equivalent value for males was 23.5% and for females the value was 34.5%.

Since 23.5% of males and 34.5% of females which fledged in the Lothians survived and bred in the Lothians and that 7.7% of males and 27.5% of females which hatched in the Lothians subsequently bred within the study area also bred at their natal territory (maximum rate of philopatry, pp.179-180), it follows that 1.8% of males and 9.5% of females which hatched in the Lothians and survived to breeding age could have bred in their natal territory i.e. minimum rates of philopatry.

Productivity of philopatric females

From the 12 breeding pairs which included a philopatric female there were 27 breeding attempts between 1985 and 1993, 6 on rivers in 2 different territories, 7 on canals in 2 different territories and 14 on still waters in 3 different territories. The mean of 1.4 cygnets fledged per pair was low when compared with 2.7 fledged per pair for all pairs throughout the study (Chapter 5, Table 20).

The breeding territories of philopatric females on still waters were all in the least productive altitude range of 0 to 50m. Low productivity was a feature also of breeding pairs on river habitat (Chapter 5, Table 27) and of the 12 breeding pairs involved in the above analysis, 9 were in territories associated with low cygnet productivity.

It was determined above (p.178) that 2.7 cygnets fledged per breeding pair resulted in over-production of birds to the age of first breeding. The 1.4 cygnets fledged per breeding pair with a philopatric female would have resulted in 0.51 cygnets to breeding age which was, never the less, in excess of that required to maintain stability in the breeding population with a mortality rate of 0.28 per breeding pair.

Breeding territory and natal site habitat of males and females

The natal site and first breeding site of the 26 males and 40 females were classified by habitat type. Among the swans which hatched and bred in the Lothians, 50% of males bred in a habitat similar to their natal habitat which compared with 80% of females. Significantly more males bred in a habitat dissimilar to their natal habitat type (Chi-squared = 6.544, df 1, $p<0.05$). Females, therefore, had a greater preference than males to breed in a territory of habitat similar in type to their natal habitat.

The mean age at first breeding for males breeding in natal habitat (3.8 years) was similar to those which bred in habitats dissimilar to natal habitat (3.7 years); figures for females were 4.3 years and 4.1 years. The preference exhibited by some individuals to breed in a territory similar in habitat to their natal territory did not cause such individuals to delay their first breeding attempt until a suitable territory became available.

The data available for 15 males and 26 females at their second breeding attempt indicated that at the second breeding attempt 53% of males and 81% of females bred in a habitat similar to their natal habitat. One female which bred for the first time on the canal did so in a non-natal territory but subsequently moved into her natal territory on the canal.

At the third breeding attempt 56% of males (n = 9) and 74% of females (n = 19) bred in a habitat similar to their natal habitat and at the fourth breeding attempt 63% of males (n = 8) and 75% of females (n = 15) bred in habitats similar to their natal habitat.

Natal territory habitat and breeding territory habitat of swans in breeding pairs

The natal site and breeding site were known for both birds in 15 breeding pairs. The type of habitat in which these pairs first bred was similar to the male natal habitat in 6 instances, similar to female natal habitat in 14 instances and similar to both male and female natal habitat in 6 instances. It was concluded that the natal habitat of the female in a breeding pair had a greater influence in the choice of breeding territory of the pair than the natal habitat of the male.

Breeding territory habitat of second generation males and females

Where the natal site of a ringed swan was known in addition to its breeding site such birds were defined for the purposes of this study as first-generation breeding birds. Ringed offspring of first-generation birds which progressed to breed were defined as second-generation breeding birds. Although there was no systematic search for breeding emigrants, 10 second-generation breeding females were recorded within the study area and none reported outside the study area while 5 second-generation males bred within the study area and 9 bred outside the study area. Of those 10 females, 6 bred in natal habitat and of the 4 which did not, 2 bred in habitat similar to maternal natal habitat. Of the 6 which bred in natal habitat the habitat type was also similar to the maternal natal habitat in 4 cases. Thus in 6 instances (60%) the habitat of a breeding female was also similar to the maternal natal habitat.

Of the 5 males which bred in the study area, 2 bred in natal habitat and of the 3 which did not, 2 bred in habitat similar to maternal natal habitat. Of the 2 which bred in natal habitat the habitat type was dissimilar to the maternal natal habitat in both cases. Thus in 2 instances (40%) the habitat of a breeding male was similar to the maternal habitat. If the males which bred outside the study area were included then 9 second-generation males (60%) bred in habitat similar to maternal natal habitat.

Inbreeding among Mute Swans hatched on canal habitat

Canal habitat occurred only in the western half of the study area and was restricted to one canal, namely the Union Canal. The Union Canal originally joined the Forth and Clyde Canal at Falkirk and thereby provided a canal link across Central Scotland from Glasgow to Edinburgh. Although the canal link is no longer intact much of the original waterway is still in existence. This is the only canal system in an area covering central Scotland, southern Scotland, Northumberland, Durham and Cumberland.

From 1978 to 1983 only one pair of Mute Swans bred on the canal in the study area and this was located at its eastern extremity at Leamington, Edinburgh. During that period, 5 cygnets fledged (all in 1981), only 0.83 cygnets fledged per breeding pair annually at that site. It was occupied continuously up to 1987 with just single cygnets fledging in 1984, 1985 and in 1986; each was colour ringed but none subsequently bred in the study area. Cygnets from the Leamington territory did not, therefore, contribute to the increase in the number of breeding pairs on the canal after 1983.

The breeding territory at Linlithgow was first occupied in 1984 and subsequent occupation was continuous. A total of 22 cygnets fledged in the four years 1984 to 1987 and a number of these birds bred in the study area, especially on the canal. Up to 6 breeding territories were occupied on the canal west of Broxburn, West Lothian from 1987. The stretch of canal between Broxburn and Leamington, at least half the total length of canal within the study area, remained unoccupied between 1978 and 1993 even though the overall breeding population had produced a surplus of swans to breeding age.

Given the tendency for both males and females to breed in natal habitat and the level of philopatry described above, in combination with the relatively restricted number of canal breeding territories, in-breeding was anticipated amongst swans on the canal. Indeed three adjacent breeding territories were utilised by six breeding pairs on the canal from 1984 to 1993 and involved three instances of in-breeding (Figure 37), including one case of incest:-

1. CSV + AZY, a grandson of ADJ and ADL with a daughter of ADJ and ADL
2. BNU + AYS/DFU, a son of ADJ and ADL with a daughter of ADJ and ADL
3. ADJ + BNA , father ADJ with a daughter of ADJ and ADL

Pairs 2 and 3 bred successfully and fledged cygnets.

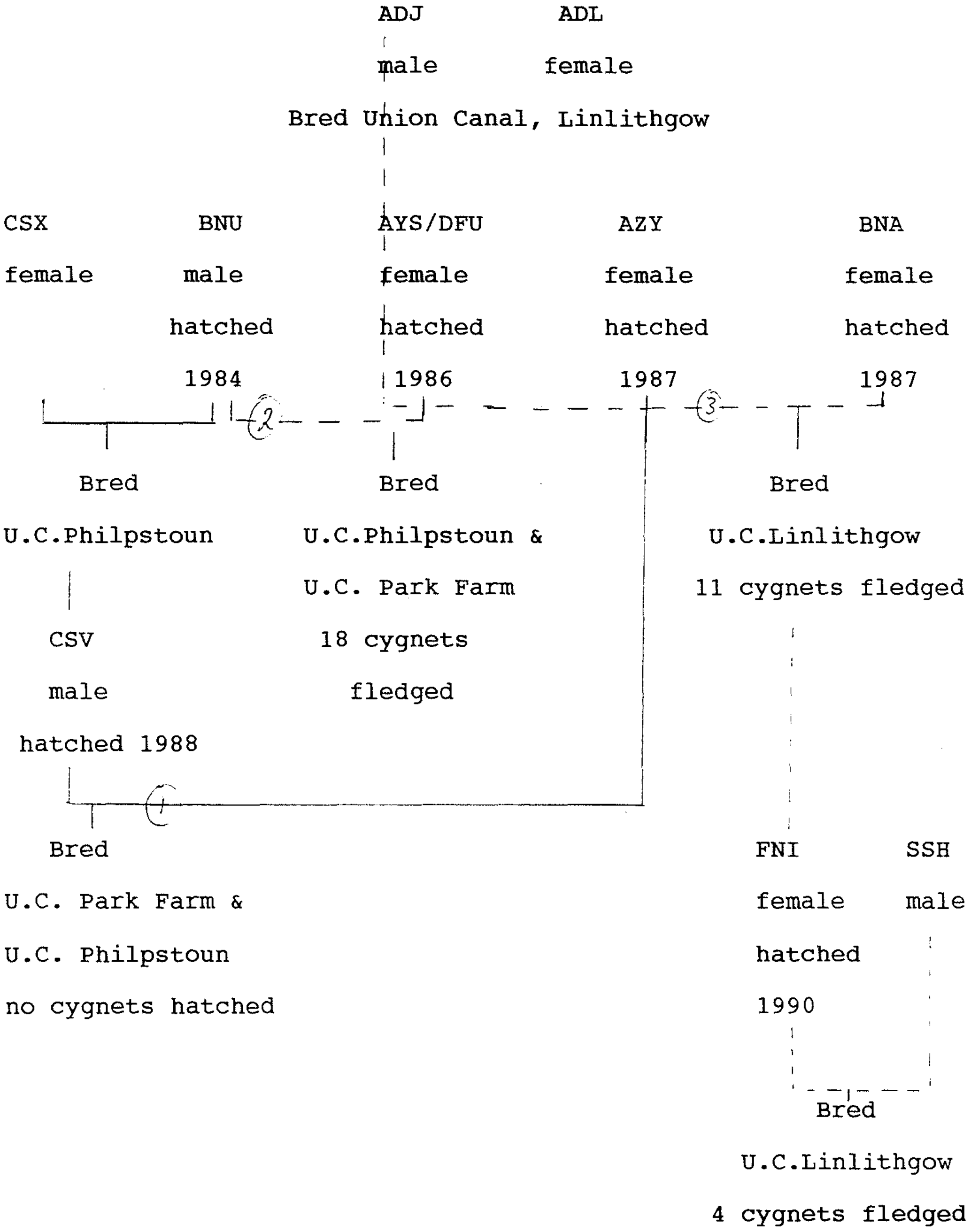


Figure 37. Inbreeding among Mute Swans on the Union Canal.

The expansion of breeding pairs along the canal appeared to have been restricted by the preference of some swans to return to natal habitat and site. If such behaviour was genetically determined then in-breeding might reinforce its continuation in the western section of the canal. In-breeding was not detected on the River Tyne where cygnet production was probably insufficient to result in sufficient swans surviving to breeding age for in-breeding to have occurred.

Immigration

In order to quantify immigration and emigration in a breeding population of swans it is necessary to ring a high proportion of cygnets which fledge from the study population and a long study period is required (Clobert and Lebreton 1991). The difficulty in achieving these requirements has resulted in both immigration and emigration being infrequently studied in detail even in other species (Harris and Wanless 1991). These requirements have been met in the present study.

Identifiable immigrants to the Lothians breeding population originated from Arbroath and Montrose in Tayside Region and Eckford in Borders Region. The level of colour ringing outside the study area was much lower than that within it; this made it impossible to accurately calculate total immigration from the number of ringed immigrants recorded breeding in the Lothians. Calculation of immigration was, therefore, based on the total number of breeding birds and the number of Lothians hatched and ringed breeding birds. It is recognised within the calculation that not all cygnets fledged in the Lothians were colour ringed and that

a proportion of these non-ringed birds would also be present in the breeding population in the Lothians.
Data for the years prior to 1991 were too few to enable an estimation of immigration, therefore analyses were restricted to the years 1991, 1992 and 1993.

Calculation of the number of Lothians hatched birds breeding in the study area.

Year	1991		1992		1993	
A. Number of breeding swans						
	male	female	male	female	male	female
	48	48	51	51	56	56
B. Number of breeding swans fledged and ringed in Lothians	11	22	11	24	19	29

Calculation of the number of breeding birds hatched in Lothians but not ringed.

C. The age range, in years, of the birds in B.						
	2-9	3-9	3-10	3-10	3-11	3-11

Of the swans which bred in 1991, the males had hatched in the years 1982 to 1989 and the females in the years 1982 to 1988.

During the period 1982 to 1989, 69.9% of fledged cygnets had been colour ringed, the equivalent figure for the period 1982 to 1988 was 69.7% (Chapter 6, Table 34). Swans which bred in 1992 had hatched in the years 1982 to 1989; during that period 69.9% of fledged cygnets had been colour ringed. Swans which bred in 1993 had hatched in the years 1982 to 1990; during that period 72.5% of fledged cygnets had been colour ringed.

D. The estimated number of Lothians fledged, but unringed, breeding swans.

Year	1991		1992		1993	
	male	female	male	female	male	female
	4.7	9.6	4.7	10.3	7.2	11.0

E. The breeding population would have included a few swans over the age of 9 years in 1991, over 10 years in 1992 and over 11 years in 1993 (Figures 31 to 34). These birds would have fledged prior to the commencement of ringing in 1982. Although the numbers of birds involved would have been small, the following are added as compensation for their omission :-

Estimated additional swans

Year	1991		1992		1993	
	male	female	male	female	male	female
	2	2	1	2	1	1

F. Total number of swans hatched in the Lothians and recorded in the breeding population (B+D+E).

Year	1991		1992		1993	
	male	female	male	female	male	female
	18	32	16	36	27	41

Calculation of immigration

G. Percentage of immigrants in the breeding population 100[1-(F/A)].

Year	1991		1992		1993	
	male	female	male	female	male	female
	62.5	33.3	68.6	29.4	51.8	26.8

H. Mean proportion of immigrants in the breeding population, 1991 to 1993. Combined sexes 45.4%

Males 61.0% Females 29.8%

I. Number of swans breeding in the study area but fledged and ringed outside the Lothians.

Year	1991		1992		1993	
	male	female	male	female	male	female
	4	2	3	2	3	1

J. Mean percentage immigrants 1991 to 1993 based only on the number of ringed immigrants.

Males 6.4% Females 3.2%

Comparison of results in J. with results in H. confirmed that calculation of immigration based solely on the number of ringed immigrants was not a precise approach to quantifying immigration.

Emigration

A total of 27 swans fledged and ringed in the Lothians were recorded breeding in Tayside, Fife, Borders, Central Region and Strathclyde Region between 1982 and 1993. Such widespread and distant emigration constituted too large an area to regularly and systematically search for ringed breeding birds. Consequently, emigration was calculated indirectly from the total number of Lothians hatched birds surviving to breeding age and the number of those swans which bred in the Lothians.

A. The percentage of Lothians hatched swans which survived to breeding age and bred in the Lothians (pp.183-4) :-

Males 23.5% Females 34.5%

B. The percentage of Lothians hatched swans which survived to breeding age and could have bred outside the Lothians (emigrants) :-

Males 76.5% Females 65.5%

There was, however, an assumption that all birds which survived to breeding age did breed. This assumption has not been substantiated in the present study and it must be surmised that some swans never bred. The figures given above regarding emigration were, therefore, figures of maximum emigration or a combination of emigration and birds which had never bred since it was impossible to separate the two categories.

Comparable immigration and emigration data were few. Immigration in the Lothians breeding population was higher than at Abbotsbury where it was estimated at 25% between 1969 and 1980 (Perrins and Ogilvie, 1981). A change in the management of the colony since 1974 resulted in a greater proportion of cygnets fledging which in turn probably contributed to the decline in immigration to about 15% for males and about 5% for females by 1992 (Perrins et al. 1994). It was also substantially greater than the 5% calculated for the South Staffordshire population by Coleman et al. (1991). The number of emigrant breeding birds from South Staffordshire was also low, although not quantified.

No Mute Swan ringed in the Hebrides has been reported breeding outside that study area (C. J. Spray pers. comm.), although there had been no systematic search for emigrants.

Absence and return of established breeding swans

Minton (1971) noted the presence of birds which had bred in previous years in non-breeding flocks in spring. Birds which had bred, but were considered to be too old to continue breeding, were recorded in moulting flocks in Sweden by Mathiasson (1981a).

In the present study a number of swans observed breeding one year were absent from the breeding population in the following year but returned to the breeding population in a subsequent year. The number of birds which left temporarily and the number which left permanently (Figure 1) require to be quantified since a net loss constituted a further parameter in the dynamics of the Lothians Mute Swan breeding population. No swan which left the breeding population was reported breeding outside the study area in a subsequent season although some were recorded in a number of different flocks, both inside and outside the study area, in subsequent seasons.

There were two principal reasons why swans left the breeding population. Firstly, some pairs bred one year, maintained a territory during the following breeding season but did not breed. Secondly, following the death of their mate from the preceding breeding season not all surviving birds managed to re-pair by the following breeding season.

The number of ringed birds which left the breeding population each year was determined for the period 1982 to 1993. As ringing of breeding birds commenced in 1982, then 1984 was the first year for which the number of swans which returned to the breeding population could be determined; the number of birds which returned was determined for the period 1984 to 1993 (Table 68).

Table 68. The number of colour ringed swans which left the breeding population each year and the number which returned to the breeding population each year, from 1982 to 1993.

Year	No. breeding, colour ringed birds		No. breeding colour ringed birds which did not breed the following year		No. colour ringed birds which returned to the breeding population.	
	Males	Females	Males	Females	Males	Females
1982	12	10	6	3	-	-
1983	6	9	0	1	-	-
1984	14	12	2	2	3	1
1985	17	14	0	1	0	0
1986	20	19	2	3	2	3
1987	23	20	1	2	0	0
1988	26	21	1	3	0	2
1989	27	25	2	1	0	2
1990	34	35	2	7	0	1
1991	38	37	4	1	1	1
1992	43	41	3	3	1	4
1993	45	47	5	4	1	1

Swans which left the breeding population

Many pairs which bred in 1982 failed to breed during the particularly wet spring of 1983 and consequently the percentage of 1982 breeding birds which had left the breeding population by the 1983 breeding season was high (Figure 38).

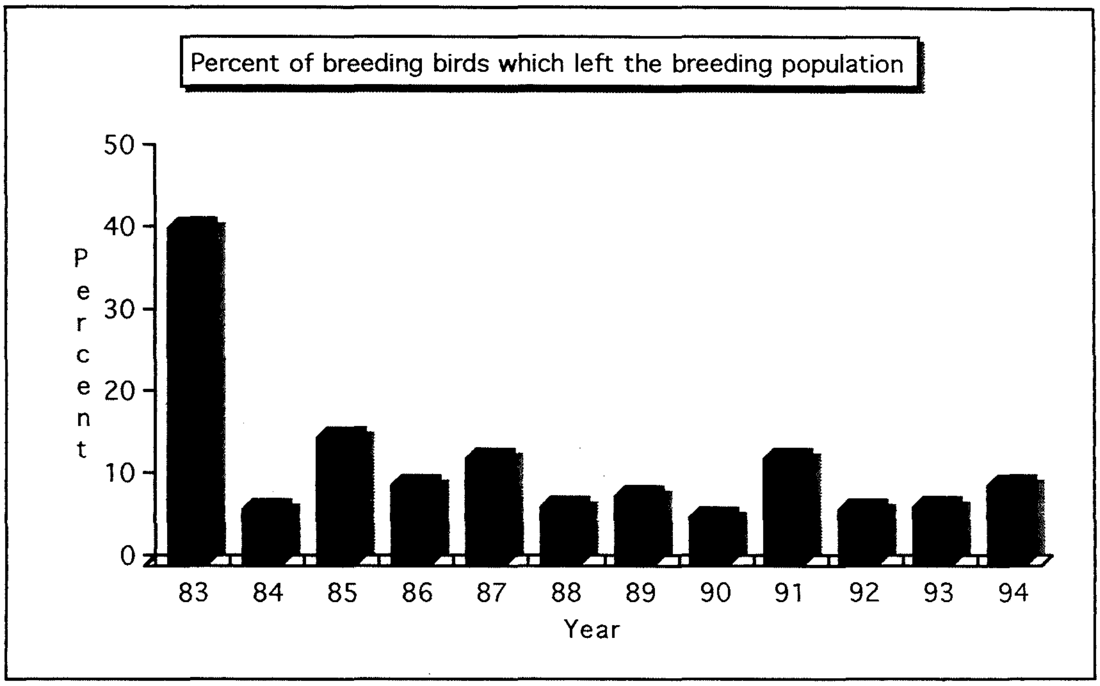


Figure 38. The proportion of breeding swans which left the breeding population.

A mean of 12.0% of breeding birds left the breeding population annually between 1982 and 1993, comprising 10.4% males and 13.3% females (Table 68). This greater proportion of females probably resulted from greater mortality among breeding males (15.1%) than among breeding females (13.5%) (Table 66), causing surviving females to leave the breeding population to seek a new mate.

Swans which returned to the breeding population

In all but two instances, birds which were absent from the breeding population and subsequently returned were absent for just one season. The two exceptions involved two females which were each absent for two breeding seasons. Of the birds which left for a single season one female left and returned three times, one male left and returned twice, one male and two females left twice and returned once. Therefore, the 8 instances in which males returned to breed involved 7 individuals and the 15 instances in which females returned to breed involved 13 individuals. After entering the breeding population there was no tendency for the majority of individuals to persistently leave and rejoin the breeding population.

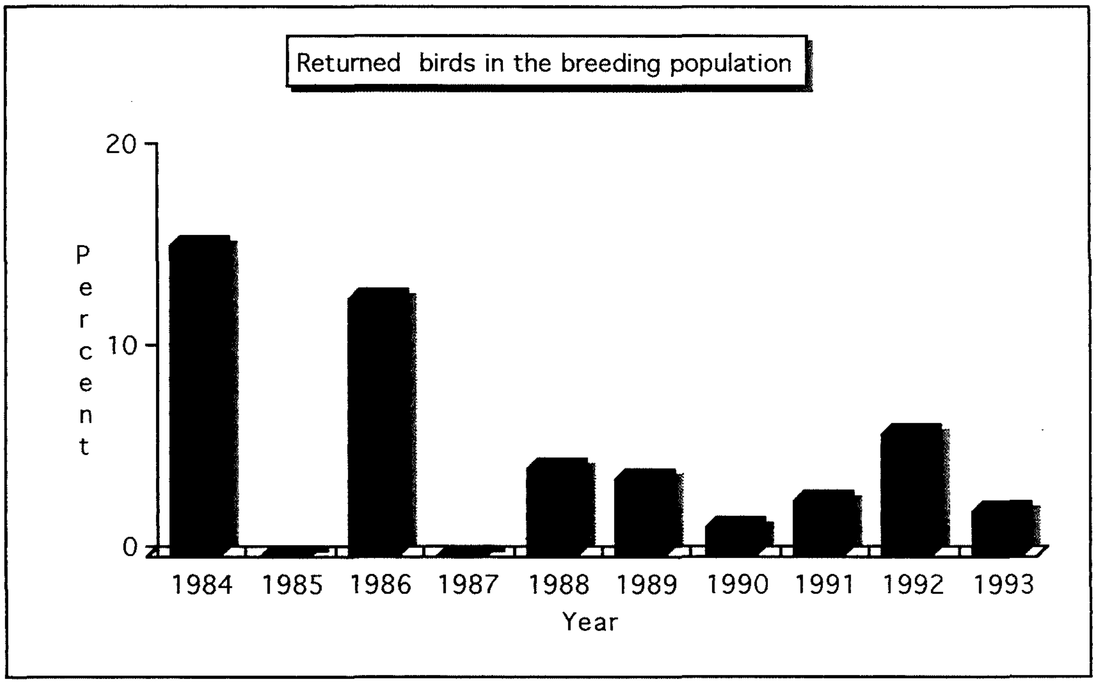


Figure 39. The proportion of swans which returned to the breeding population

The relatively high proportion of birds which returned to the breeding population in 1984 reflected the return of the high number of 1982 breeding birds which were absent in 1983 (Fig. 39). Similarly, the 1986 result reflected the return of 1984 and 1985 absentees since no birds returned

in 1985.
The annual mean of returning birds in the breeding population was 4.6% males and 5.9% females; the overall mean was 4.9% (Table 68). The lower proportion of males which returned to the breeding population was probably due to greater mortality amongst breeding males than females.

Of the 8 instances where males returned to breed, 7 (87.5%) returned to their last breeding site. Similarly, of the 15 instances where females returned to breed, 10 (66.7%) returned to their last breeding site. The failure of birds to re-occupy their previous breeding site was primarily due to a new pair having taken up occupancy of the site in the intervening years.

Comparable swan data were available only in Perrins and Ogilvie (1981). Their data from the Abbotsbury and Radipole study between 1974 and 1979 indicated that 18.7% of birds in the Abbotsbury breeding population and 24.9% of birds in the Radipole breeding population left and did not return to the breeding population in subsequent years. These figures were high in comparison with the 7.1% estimated for the Lothians population.
Newton (1989b) concluded that the occurrence of non-breeding years was common among established breeding birds of species which were subject to annual fluctuations in environmental conditions and among long-lived species which experienced more stable conditions. It was clearly a parameter not confined to Mute Swan populations and estimated values for the present study were of a size to have a considerable effect on a population's ability to sustain itself.

In addition to the loss due to mortality, the Lothians breeding population was subject to a net annual loss of 5.8% males and 7.4% females due to swans permanently leaving the breeding population.
When compared with results from Abbotsbury the loss from the Lothians breeding population was comparatively low. A direct comparison with the Abbotsbury population findings may, however, be inappropriate as the Abbotsbury breeding birds were subject to human interference to a degree not experienced in other British Mute Swan populations (Perrins et al. 1994).

There were no records of divorce among established breeding pairs during the thirteen years of the study. Minton (1968) estimated a 3% divorce rate among swans in South Staffordshire during the period 1961 to 1967 while Birkhead and Perrins (1986) indicated that divorce among Mute Swans was unusual.

Discussion

The breeding season is regarded as a time of stress for the birds involved when females in particular can lose up to one third of body weight (Birkhead and Perrins 1986). Given that there was no significant difference in mortality between males and females in the breeding population then territorial defence, undertaken primarily by males, is probably as demanding as egg laying and incubation.

Mortality was relatively high during the first two years after fledging (Chapter 6). Mobility of age cohorts ringed in the Dublin area was investigated by Collins and Whelan (1994). They found that mobility was greatest in the first year cohort and the distance travelled was greatest in the second year. It was demonstrated that few birds commenced breeding in the Lothians at the age of two years but the majority commenced from the age of three years and birds which did breed tended to do so for the remainder of their lives. Higher mortality in the fledged population in general than in the breeding population was probably associated with the more mobile non-breeding one and two year age classes of the population. There was no indication that birds became too old to breed as reported by Mathiasson (1981a), at least up to the age of eleven years.

The majority of breeding pairs of swans in the study area remained faithful to the territory in which they first bred as a pair. In some instances breeding birds changed breeding site but this normally followed mate loss and re-pairing. Harris and Wanless (1991) found that once a pair of Puffins had bred they rarely moved to another area of the colony or to a different colony even if conditions appeared unfavourable at their chosen site. In contrast, some female Sparrowhawks in southern Scotland were found to move from poor breeding territories to higher quality territories in subsequent breeding seasons (Newton 1989a). The initial choice of breeding territory could, therefore, affect the long term reproductive output of breeding swans since some breeding territories were less productive than others. If there was potential for greater life-time reproduction by breeding in the natal site or in a habitat similar to natal habitat then it would seem beneficial to breeding pairs to delay acquisition of a breeding territory until an appropriate site could be occupied. There was, however, no evidence to suggest that such a delay occurred. It may have been the case that mortality in the breeding population was too low for this to be a beneficial strategy since the delay might have been considerable with the possibility of death in the intervening years. The number of productive years would also have been considerably reduced, although this in turn might be compensated for if productivity increased with age.

The degree of philopatry and preference to breed in a habitat of similar type to natal habitat in the Lothians did not appear to inhibit the overall numerical increase in the population. There was, however, evidence to suggest that expansion might have been inhibited on the canal, and that philopatry led to in-breeding and incest. In-breeding and incestuous breeding did not appear to impart any disadvantage to the birds involved in terms of productivity.

Incest was recorded in the South Staffordshire study area (Coleman et al. 1994) with 7 instances from 1389 pairs, all of which occurred at the siblings' natal site. Coleman and Minton (1979) described the South Staffordshire swan population as parochial. Coleman et al. (1991) determined a low level of immigration in that breeding population where 13% of breeding males and 36.5% of breeding females bred within 1.6 km of natal site (Coleman and Minton 1979). Philopatry was not quantified in that study, but it undoubtedly contributed to the occurrence of incest in the breeding population.

Both colonial and non-colonial breeding swans were monitored in the Copenhagen study area of Bacon and

Andersen-Harild (1989). They estimated that 50% of colonial breeders had hatched in territories but no territorial breeders hatched in colonies and concluded that this pattern was to some extent genetically determined.
Coulson (1991) suggested that philopatry was genetically controlled. He found that less than 30% of Herring Gulls ringed as chicks on the Isle of May which survived to breeding age actually bred in their natal colony. In contrast to findings in the Lothians Mute Swan population, philopatry was more pronounced in male than female Herring Gulls.
In the case of the Lothians population there was an indication that the choice of breeding territory was inherited, at least with regard to the type of habitat associated with the territory. Once fledged, many cygnets were never subsequently recorded at the natal site. If they had learned to recognise their natal site during the pre-fledging period it would have seemed unlikely that these birds could have retained such information for a number of years prior to their return to breed at their natal site or in the natal type of habitat. The choice of breeding territory was more likely to have been genetically determined.

Coulson (1991) described changes in immigration and emigration rates in gull populations which resulted from long-term culling on the Isle of May, Fife. The disturbance caused by culling in the gull colony resulted in an increase in emigration and probably contributed to an unwanted increase in the number of Lesser Black-backed Gulls *Larus fuscus* in the Netherlands. Failure to include immigration and emigration in the consideration of any population management techniques regarding Mute Swan populations would probably render the techniques ineffective in the long term while their exclusion from calculations relating to the breeding population dynamics would render the results inaccurate.

The wide geographical range of both the origins of immigrants and the location of breeding territories of emigrants, in conjunction with calculated levels of immigration and emigration, indicate that mixing of swans from eastern and central Scotland occurred in the Lothians breeding population. In addition, results showed that mixing occurred throughout the wider area of eastern and central Scotland. These findings contrast with the more sedentary nature of some English populations (Coleman et al. 1994) and contradict the views of Kirby et al. (1994) that Mute Swans in Britain were generally resident, with little movement of birds between different areas of the country nor between locations within those areas.

It appeared that, based on the balance between recruitment and mortality, the Lothians population could have tolerated a considerable range in many of its demographic parameters while maintaining a stable breeding population. Indeed, there appeared to be a surplus of potential breeding birds which might have been sufficient to account for the increase in the number of breeding pairs between 1982 and 1993. A number of additional parameters did, however, require to be taken into consideration since their estimated values were such that they could have had a significant effect on the population's ability to maintain, or additionally account for the increase in, the number of breeding birds. The parameters which affected the balance in the number of swans in the Lothians breeding population are, therefore, demonstrated in a model in the following chapter.

Chapter 8

The demographic parameters which effected change to the number of breeding pairs of Mute Swans in the Lothians

Introduction

The demographic parameters which determined the number of Mute Swans which bred in the Lothians have been quantified in earlier chapters. The results from those chapters will be utilised in the present chapter in order to determine whether or not the breeding population was, as a consequence of its own productivity, capable of maintaining its numbers. In addition, the extent to which the increase in the number of breeding swans was dependent on immigration will be investigated.
Determination of values for demographic parameters below which the population could no longer be self-sustaining, is explored also. Perrins (1991) suggested critical values for some parameters but took no account of other parameters in his calculations.

Results

The demographic parameters which effectively controlled the size of the breeding population are illustrated diagrammatically in Figure 40.

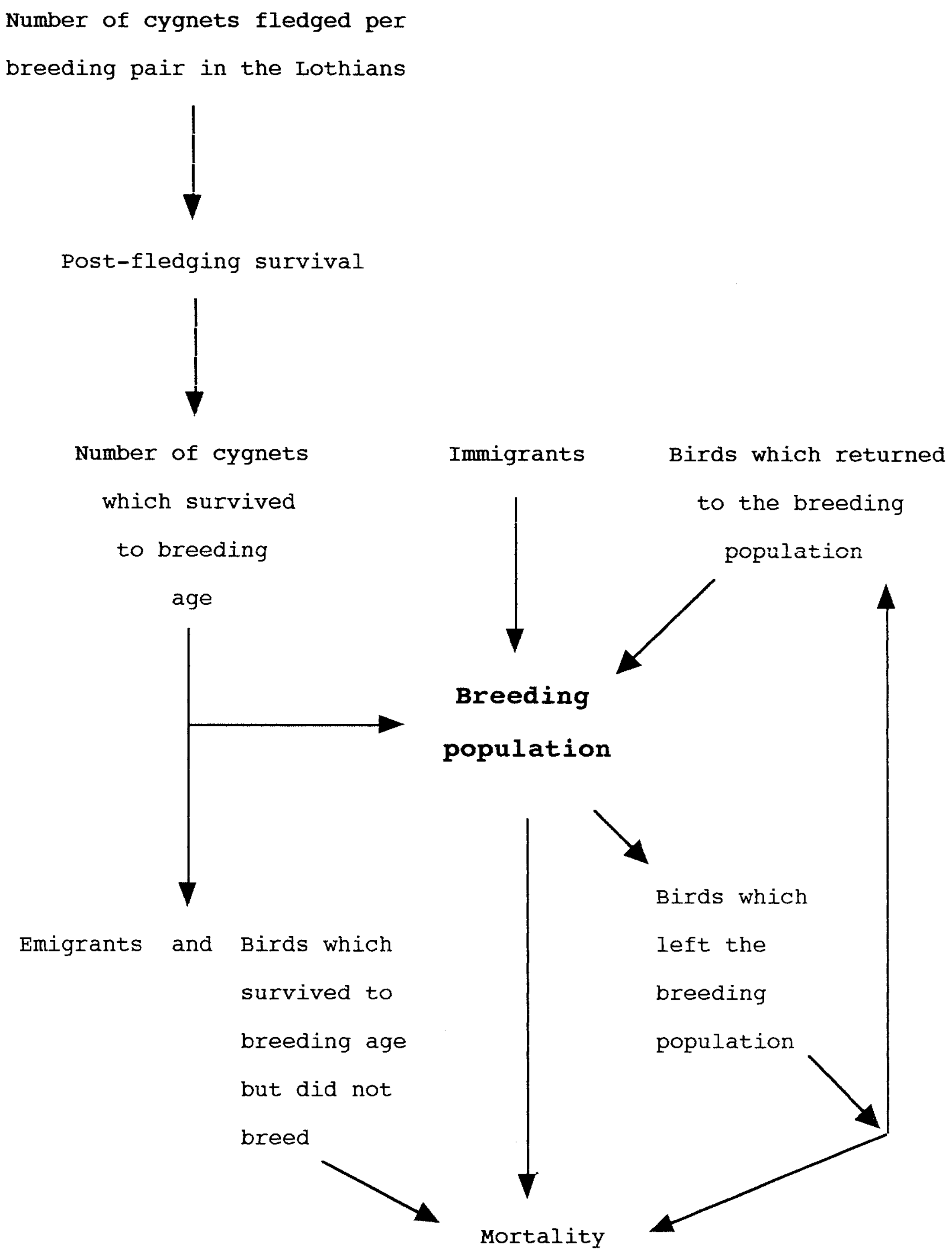


Figure 40. Parameters which effectively caused an increase, a decrease or stability in the number of pairs of Mute Swans which bred in the Lothians.

In order to assess the percentage change in the number of swans which bred in the study area, the following three models were developed, based on the parameters illustrated in Figure 40.

The continued presence of immigrants in the breeding population depended upon immigrant breeding birds which subsequently died being replaced by new immigrants and not by Lothians hatched, intrinsic, birds. In the following calculations, therefore, the breeding population was subdivided into intrinsic and immigrant birds.

In Model 1 sexes are combined in order to assess the overall balance in the intrinsic segment of the breeding population. Differences between sexes are investigated through Models 2 and 3.

Model 1. Combined sexes

Calculations based on 100 breeding birds (50 breeding pairs).

- The 100 breeding swans comprised 45.4% immigrants (Chapter 7, p194) or 54.6% non-immigrants. Of the 100 breeding swans, 54.6 hatched in the Lothians (intrinsic segment).

- Mortality was 14.3% (Chapter 7, p177); the number of deaths amongst the intrinsic segment was 14.3% of 54.6 7.8

- Loss due to swans leaving (12.0%) (Chapter 7, p199) and some returning (4.9%) (Chapter 7, p201) was 7.1% of 54.6 3.9

Annual loss amongst the intrinsic segment of
the 100 breeding birds **11.7** swans

- Number of cygnets produced per breeding pair which survived to breeding age was 0.96 (Chapter 7, p175); the number of cygnets from 50 pairs was 48.0.

- Emigration/birds which never bred (Chapter 7, p195) was 70.8%, thus 29.2% of 48.0 bred in Lothians
14.0

Annual gain amongst the intrinsic segment of
the 100 breeding birds **14.0** swans

Therefore, there was a mean annual change in the intrinsic breeding population of 14.0 - 11.7 = + 2.3 birds per 100 breeding birds.
Thus, based on an annual rate of increase in the breeding population of 9% this represents a 2% annual increase in the intrinsic portion of the breeding population and a 7% increase per annum in the immigrant portion of the breeding population.

It was concluded that productivity in the Lothians was sufficient to sustain the breeding population and to account for a 2% annual increase in the number of breeding birds. However, productivity was not sufficient to achieve the 9% mean annual increase in the breeding population which occurred during the period 1978 to 1993 (Chapter 4). That increase was achieved primarily through the 7% annual increase in the number of immigrant swans which bred in the study area.

Model 2. Males

Calculation based on 100 breeding males.

- The male breeding population comprised 61.0% immigrants (Chapter 7, p194) or 39.0% non-immigrants. Thus 39 of the 100 breeding males hatched in the Lothians.

- Mortality was 15.1% (Chapter 7, p177); the number of deaths amongst the intrinsic segment of 100 males was 15.1% of 39 5.9

- Loss due to swans leaving (10.4%) (Chapter 7, p199) and some returning (4.6%) (Chapter 7, p201) was 5.8% of 39 2.3

Annual loss amongst the intrinsic segment of the 100 breeding males **8.2** swans

- Number of male cygnets produced per breeding pair which survived to breeding age was 0.53 (Chapter 7, p175); the number of cygnets from 100 breeding males was 53

- Emigration/birds which never bred was 76.5% (Chapter 7, p195), thus 23.5% of 53 bred in Lothians 12.5

Annual gain amongst the intrinsic segment of the 100 breeding males **12.5** swans

Therefore, there was a mean annual change in the intrinsic male breeding population of 12.5 - 8.2 = + 4.3 males per 100 breeding males.

Thus, based on an annual rate of increase in the breeding population of 9% this represents a 4% annual rate of increase in the intrinsic portion of the male breeding population and a 5% increase per annum in the immigrant portion of the male breeding population.

Productivity in the Lothians was sufficient to sustain the male breeding population and to account for a 4% annual increase in the number of breeding males. However, productivity was insufficient to achieve the 9% annual increase in the number of breeding males which occurred during the period 1978 to 1993 (Chapter 4). That increase was achieved in conjunction with the 5% annual increase in the number of immigrant males which bred in the study area.

Model 3. Females

Calculation based on 100 breeding females.

- The female breeding population comprised 29.8% immigrants (Chapter 7, p194) or 70.2% non-immigrants. Thus 70.2 of the 100 breeding females hatched in the Lothians.

- Mortality was 13.5% (Chapter 7, p177); the number of deaths amongst the intrinsic segment of 100 females was 13.5% of 70.2 9.5

- Loss due to swans leaving (13.3%) (Chapter 7, p199) and some returning (5.9%) (Chapter 7, p201) was 7.4% of 70.2 5.2

Annual loss amongst the intrinsic segment of
the 100 breeding females **14.7** swans

- Number of female cygnets produced per breeding pair which survived to breeding age was 0.43 (Chapter 7, p175); the number of cygnets from 100 females was 43.

- Emigration/birds which never bred was 65.5% (Chapter 7, p195); thus 34.5% of 43 bred in Lothians 14.8

Annual gain amongst the intrinsic segment of
the 100 breeding females **14.8** swans

Therefore, there was a mean annual change in the intrinsic female breeding population of 14.8 - 14.7 = + 0.1 females per 100 breeding females.
Thus, based on an annual rate of increase in the breeding population of 9% this represents no annual increase in the intrinsic portion of the female breeding population and a 9% increase per annum in the immigrant portion of the female breeding population

Productivity in the Lothians was sufficient to sustain the female breeding population. However, productivity was insufficient to achieve an increase the number of breeding females. Thus, the 9% annual increase which occurred during the period 1978 to 1993 (Chapter 4) was achieved solely by an increase in the number of immigrant females which bred in the study area.

The effect on the intrinsic segment of the breeding population of a change in the values for the demographic parameters

Models 1 to 3 were transformed onto a spreadsheet in Claris Works. This spreadsheet format enabled calculation of the percentage change in the size of the intrinsic proportion of the breeding population by substituting a range of values for either a single parameter or number of parameters, within each Model.

Variation in productivity

Estimates of productivity for breeding pairs in different categories of breeding territory habitat, determined in previous chapters, were substituted in the models in order to determine the change which would occur in the size of the breeding population if those values were applied throughout the study area (Table 69).

Table 69. The expected change in the breeding population if productivity from canal, river and still water breeding territories were applied generally in the study area.

Stage in cygnet development	Productivity per breeding pair, categorised by breeding territory habitat								
	Canal			River			Still waters		
	m+f	m (male)	f (female)	m+f	m	f	m+f	m	f
Small	4.0			2.7			4.0		
Medium	3.5			2.2			3.3		
Large	3.4			2.0			3.0		
Fledged	3.4	1.8	1.6	2.0	1.0	1.0	2.8	1.4	1.4
First breeding, age specific	1.2	0.7	0.5	0.7	0.4	0.3	1.0	0.6	0.4
% Change in the intrinsic segment of the breeding population	6	7	4	- 1	1	- 4	3	5	1

It was apparent from Table 69 that if the level of productivity achieved by pairs which bred on canals and still waters was also achieved throughout the study area then the Lothians breeding population would have been able to sustain its numbers. The population would, however, have remained partially dependent on immigration in order to achieve a 9% annual increase. Indeed, even the high level of productivity recorded on canals was insufficient to achieve a 9% annual increase in the breeding population. If the level of productivity on rivers was recorded throughout the study area then the Lothians breeding population would have declined by 1% per annum between 1978 and 1993 and the population would have been dependent on immigrants in order to sustain its numbers. The inadequate productivity on rivers resulted in part from the insufficient production of female cygnets.

The level of productivity on low altitude still waters was also insufficient to maintain the breeding population due to the insufficient production of female cygnets (Table 70). The productivity figure for mid altitude still waters was sufficient to maintain the breeding population and, in contrast to productivity from all the other categories of habitat, it was sufficient to account for a 9% annual increase in the breeding population.

By conveniently disregarding demographic parameters which were more difficult to quantify, such as immigration and emigration, it was suggested in Chapter 7 (p185) that the level of productivity recorded by philopatric females was in excess of that required to maintain a stable breeding population. It was apparent from Table 71 that such a low

Table 70. The expected change in the breeding population if productivity from still water breeding territories in three altitude categories were applied generally in the study area.

	Productivity per breeding pair, categorised by breeding territory habitat								
Stage in cygnet development	Still water 0-50m			Still water 51-100m			Still water 101-270m		
	m+f	m	f	m+f	m	f	m+f	m	f
Small	3.5			5.6			4.3		
Medium	2.6			5.1			3.7		
Large	2.3			4.8			3.5		
Fledged	2.1	1.1	1.0	4.6	2.4	2.2	3.4	1.8	1.6
First breeding, age specific	0.7	0.4	0.3	1.6	0.9	0.7	1.2	0.7	0.5
% Change in the intrinsic segment of the breeding population	-1	2	-3	12	13	11	6	7	4

Table 71. The expected change in the breeding population if productivity from breeding pairs which included a philopatric female was applied generally in the study area.

	Productivity per breeding pair, categorised by breeding territory habitat					
	Habitats combined			Habitats combined, each pair contained a philopatric female		
Stage in cygnet development	m+f	m	f	m+f	m	f
Small	3.7					
Medium	3.1					
Large	2.8					
Fledged	2.7	1.4	1.3	1.4	0.7	0.7
First breeding, age specific	0.9	0.5	0.4	0.5	0.3	0.2
% Change in the intrinsic segment of the breeding population	2	4	0	- 4	- 2	- 7

level of productivity was in fact insufficient to maintain a stable breeding population. Indeed, insufficient numbers of both male and female cygnets were produced.

The mean of 2.7 cygnets fledged per breeding pair resulted in an annual increase of 2.1% in the intrinsic breeding population.

If there had been no annual increase in the size of the breeding population and all parameters except productivity remained unchanged, then the population would have required to produce just 2.3 cygnets fledged per breeding pair (Figure 41). A 9% increase in the intrinsic breeding population would have required a productivity figure of 4.0 cygnets fledged per breeding pair.

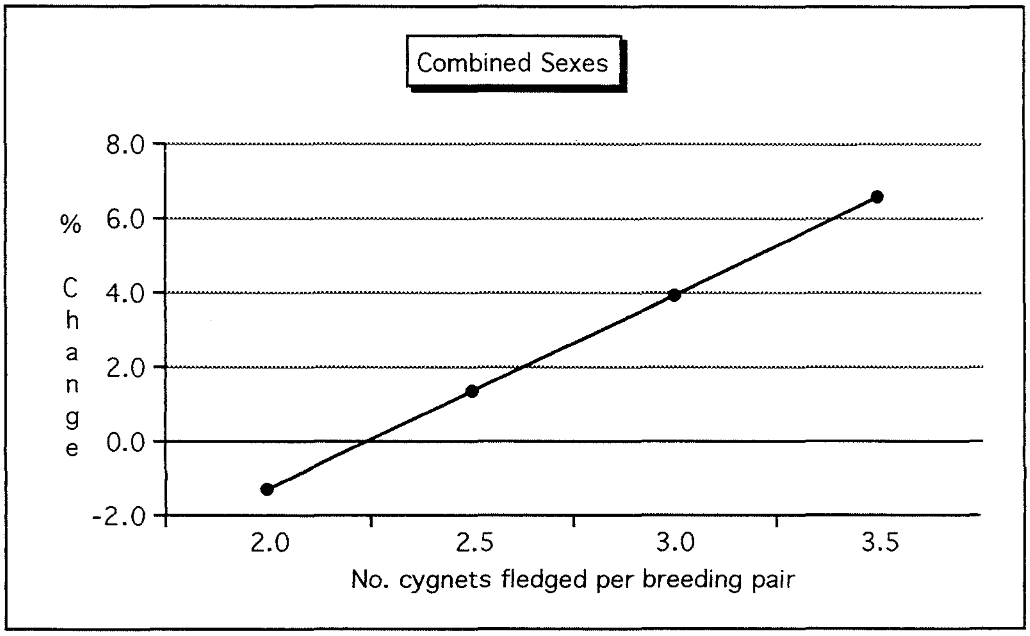


Figure 41. The change which would occur in the size of the intrinsic segment of the breeding population if there was an increase or decrease from the mean of 2.7 cygnets fledged per breeding pair for combined sexes.

The mean number of male cygnets fledged per breeding pair over all habitats was 1.4 and, as demonstrated in Figure 42, this value could theoretically be reduced to 0.9 before the number of intrinsic breeding males would decrease. In contrast, Figure 43 indicates that no decrease from the mean of 1.3 female cygnets fledged per breeding pair over all habitats could be accommodated.

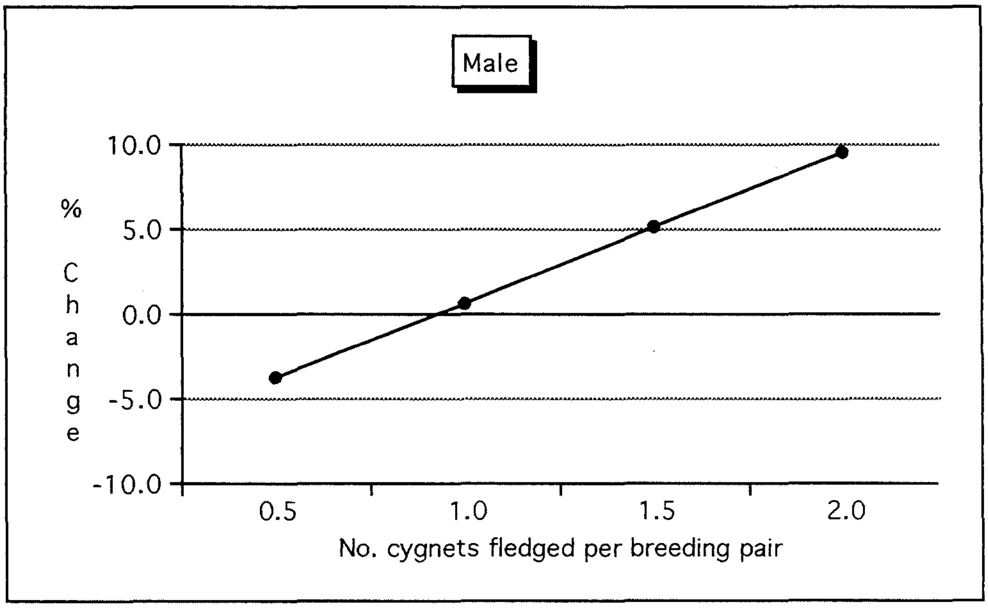


Figure 42. The change which would occur in the size of the male segment of the intrinsic breeding population if there was an increase or decrease from the mean of 1.4 male cygnets fledged per breeding pair.

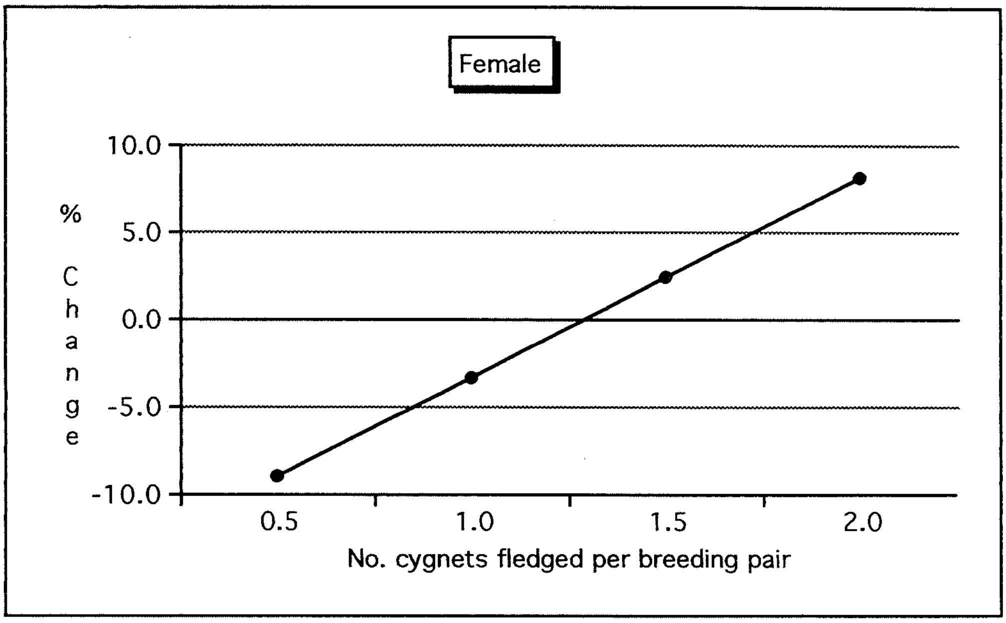


Figure 43. The change which would occur in the size of the female segment of the intrinsic breeding population if there was an increase or decrease from the mean of 1.3 female cygnets fledged per breeding pair.

Variation in mortality

There would have been no increase in the intrinsic segment of the breeding population if mortality in that population increased by 4.4% to an annual mean of 18.7% and all other parameters remained unchanged. Similarly, a decline of 12.1% in the mortality rate to an annual mean of 2.2% would have accounted for the 9% increase in the intrinsic breeding population.

It appeared that the population could have tolerated a 4.4% increase in its mean annual mortality and still remained self-sustaining. An increase in the mortality rate greater than 4.4% would have resulted in a decline in the size of the intrinsic breeding population. However, it was likely that a change in the mortality rate in the breeding population would have been apparent also in the non-breeding population since the cause of increased mortality, for example severe winter weather, would probably have affected the entire population.

Figures 44, 45 and 46 were constructed, and all subsequent calculations undertaken, by varying the mortality rate for the breeding population in addition to varying the post-fledging survival rates. For example, if a theoretical increase in the estimated rate of mortality of 1% was applied then a 1% increase was also applied to the mortality rates of each post-fledging age class.
An increase in the mortality rates of each post-fledging age class resulted in a decrease in proportional survival to breeding age and, consequently, a decrease in the number of cygnets which survived to breeding age.

It was apparent from Figure 44 that the mortality rate for combined sexes could increase by 1.9%, from 14.3% to 16.2%, before the intrinsic proportion of the breeding population would decline in numbers. The male population could have tolerated an increase of 4.7% from 15.1% to 19.8% (Figure 45) whilst the female breeding population could have tolerated an increase of 0.1% from 13.5% to 13.6% (Figure 46).

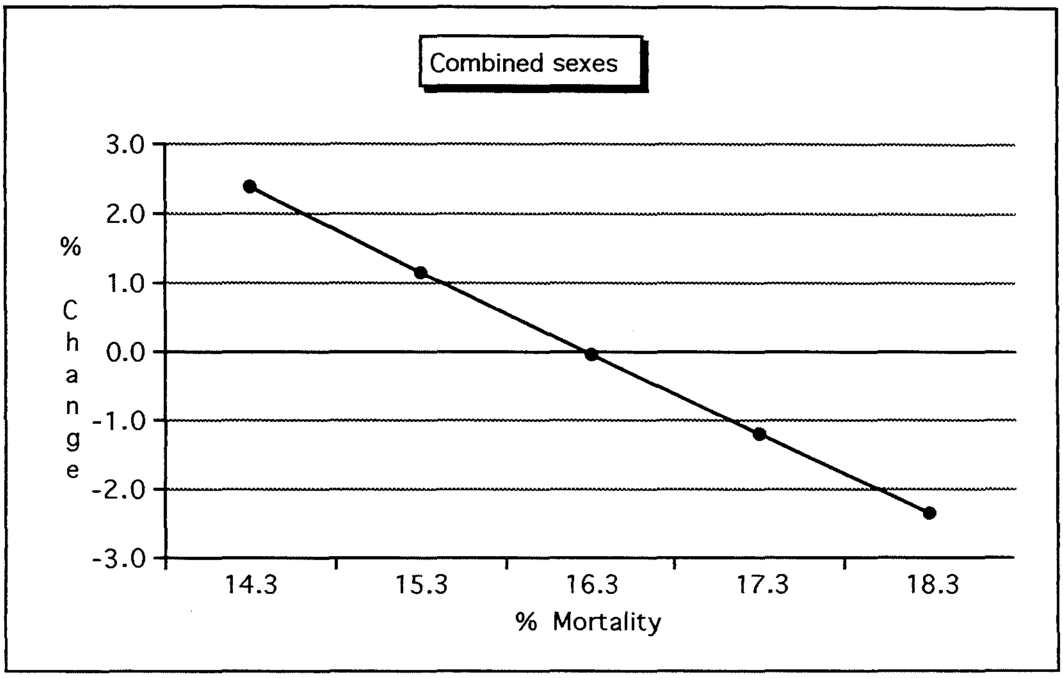


Figure 44. The change which would occur in the size of the intrinsic segment of the breeding population if there was an increase from the mean mortality of 14.3% when sexes combined.

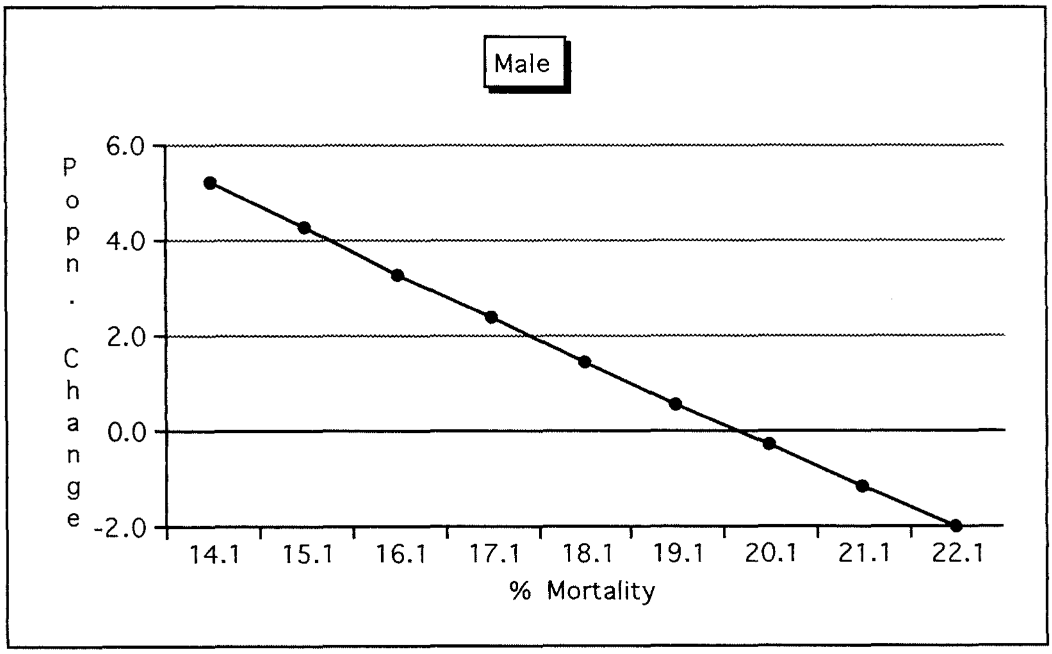


Figure 45. The change which would occur in the number of intrinsic breeding males if there was variation in mortality, from the mean of 15.1%.

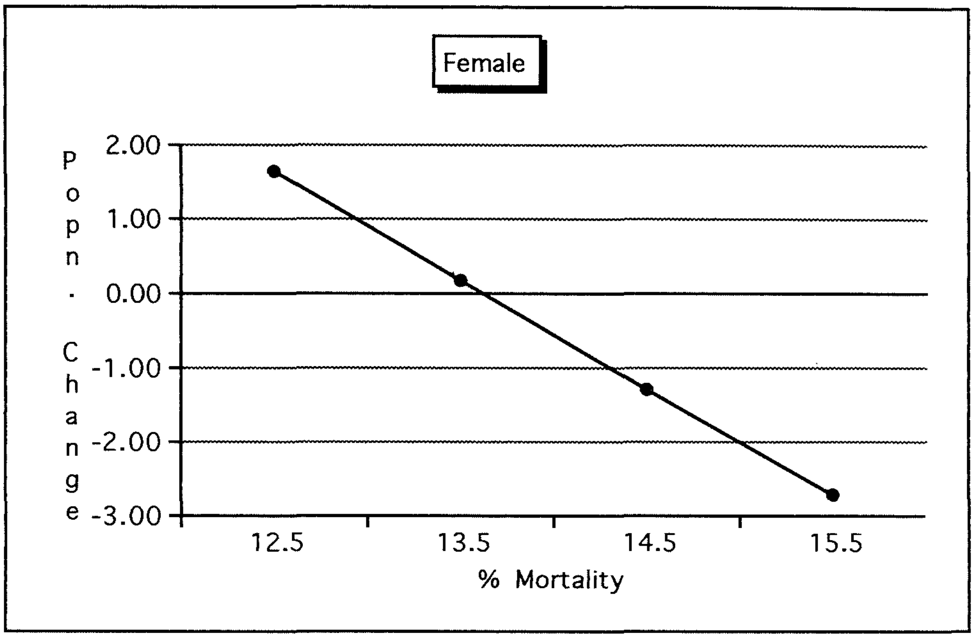


Figure 46. The change which would occur in the number of intrinsic breeding females if there was variation in mortality, from the mean of 13.5%.

By increasing mortality in the breeding population and in the post-fledging population simultaneously the 4.4% increase in mortality which the population was initially (p222) thought to be able to sustain, without the population going into decline, was reduced to 1.9%. Thus, the complex nature of the dynamics of the breeding population was apparent.

Effect of simultaneous variation in mortality and productivity

If the estimated number of cygnets fledged per breeding pair were to change then an increase or decrease may or may not occur also in the mean annual mortality figures. Figures 47, 48 and 49 illustrate the potential effects of changes in the number of cygnets fledged per breeding pair and in mortality on the percentage change to the intrinsic proportion of the breeding population. The range of values was chosen to include the mortality and productivity values in Models 1, 2 and 3, and the maximum mortality values and minimum productivity values required to maintain a stable breeding population (0.0% Change) which were deduced above.

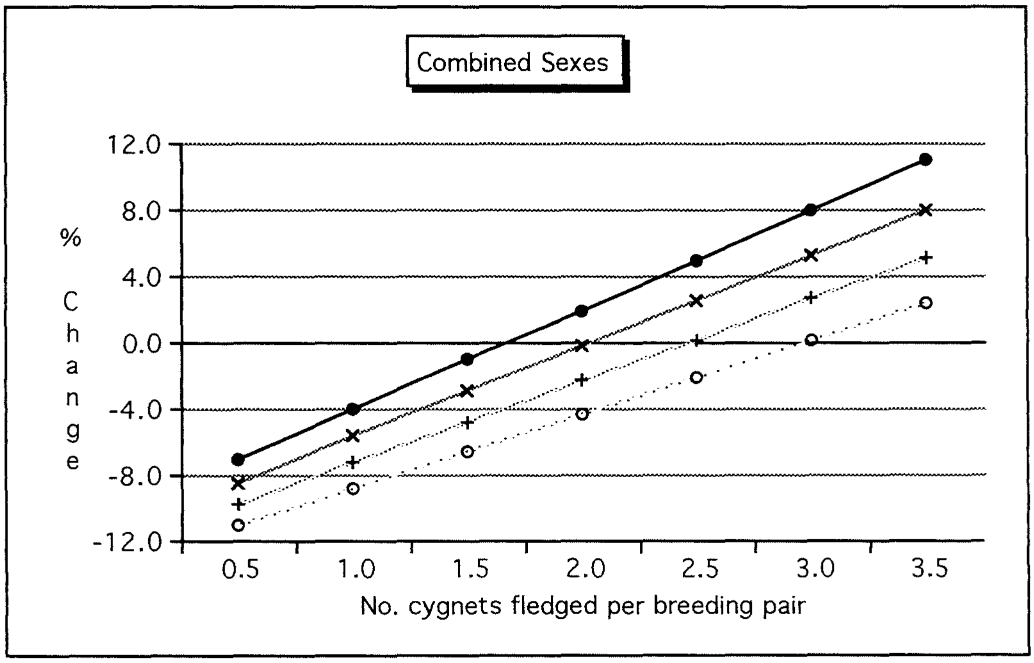


Figure 47. The percentage change expected in the intrinsic segment of the breeding population for a range of values for the number of cygnets fledged per breeding pair and a range of mortality figures. Mortality in the breeding population:- 11.3% (●), 13.3% (x), 15.3% (+) and 17.3% (o).

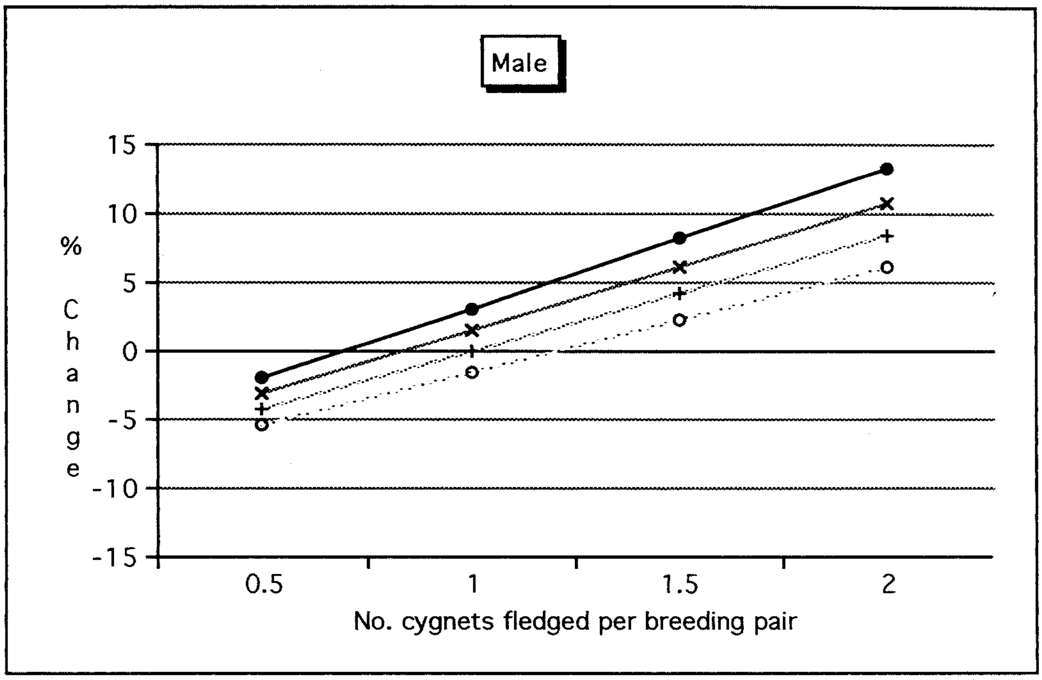


Figure 48. The percentage change expected in the intrinsic segment of the male breeding population for a range of values for the number of male cygnets fledged per breeding pair and a range of mortality figures. Mortality in the breeding population :- 12.1% (●), 14.1% (x), 16.1% (+) and 18.1% (o).

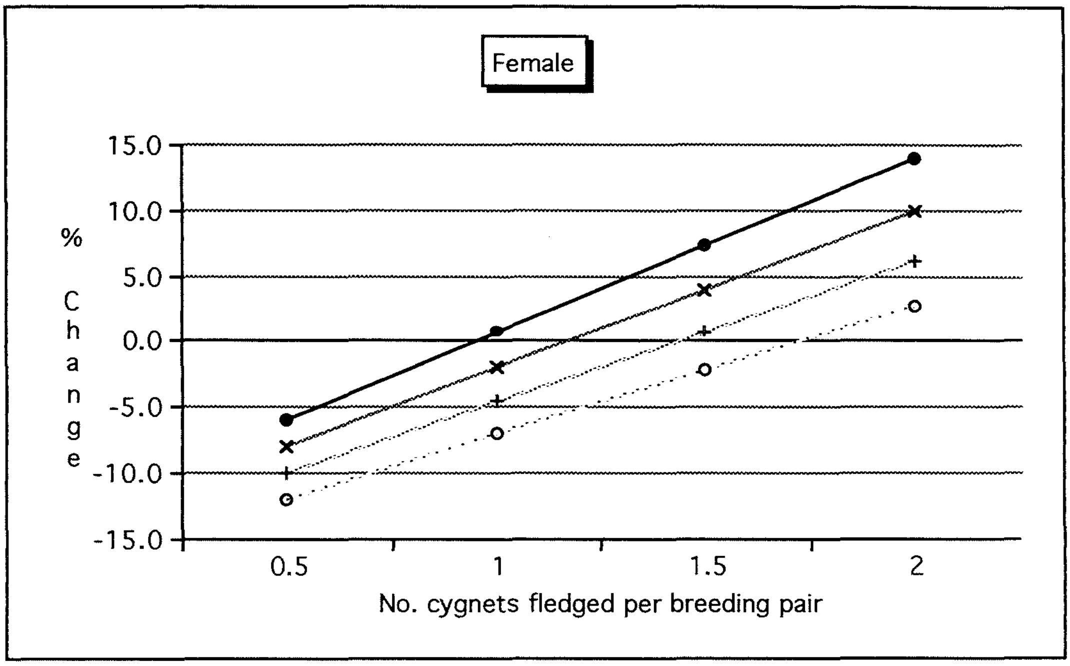


Figure 49. The percentage change expected in the intrinsic segment of the female breeding population for a range of values for the number of female cygnets fledged per breeding pair and a range of mortality figures. Mortality in the breeding population :- 10.5% (●), 12.5% (x), 14.5% (+) and 16.5% (o).

A visual scan, horizontally along the 0.0 % change grid lines, revealed that the linear plots for males (Figure 48) were more closely aligned than the linear plots for females (Figure 49). For each 1% increase in mortality the female population required more cygnets fledged per breeding pair than the male population, in order to achieve stability in the size of its intrinsic breeding population. This was partially a consequence of lower emigration amongst females which resulted in a greater proportion of intrinsic females than intrinsic males in the breeding population. Therefore, more recruits were required to replace the greater number of birds lost through, for example, mortality. The remaining demographic parameters also influence this difference to varying degrees.

Figures 50, 51 and 52 show, more clearly, the line of zero change in Figures 47, 48 and 49. If other combinations of productivity and mortality values were to occur during the study and their plots fell above the line then the population could be expected to increase; if the plots fell below the line then the population would decline.

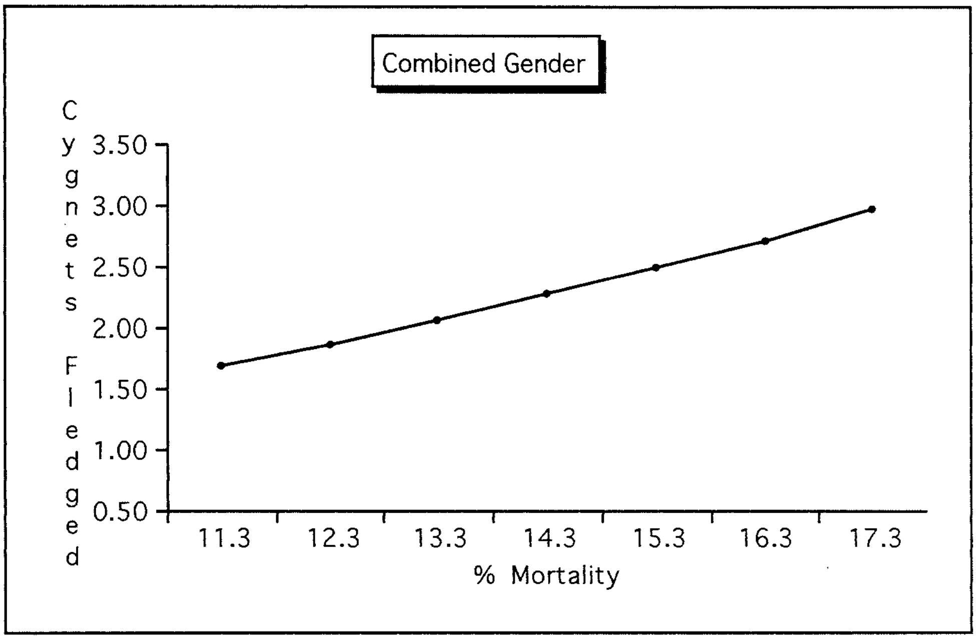


Figure 50. The line of zero change in the number of breeding swans.

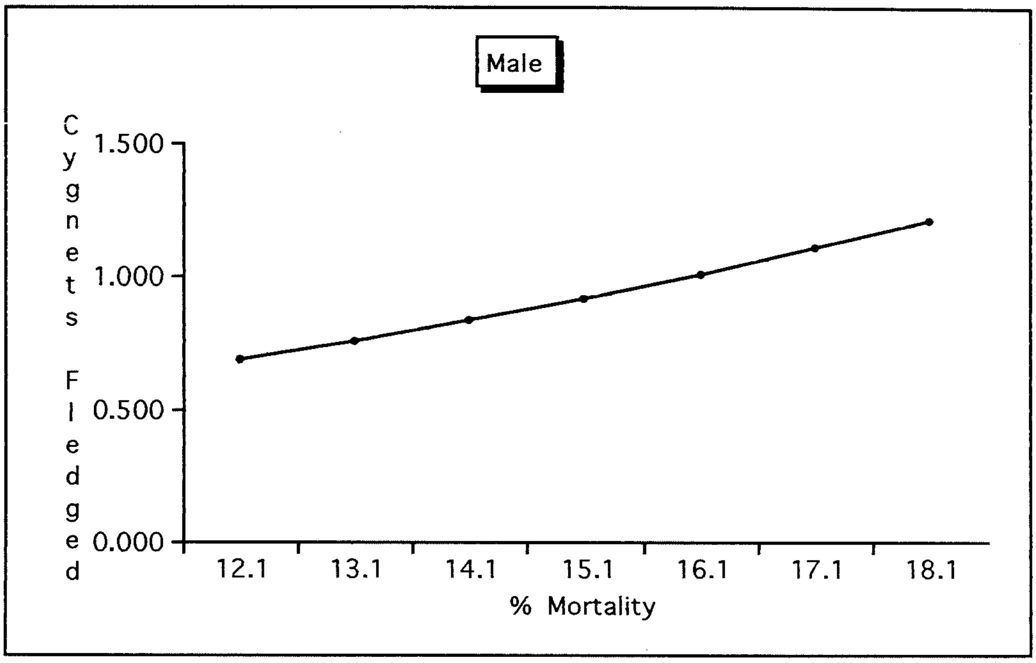


Figure 51. The line of zero change in the number of male breeding swans.

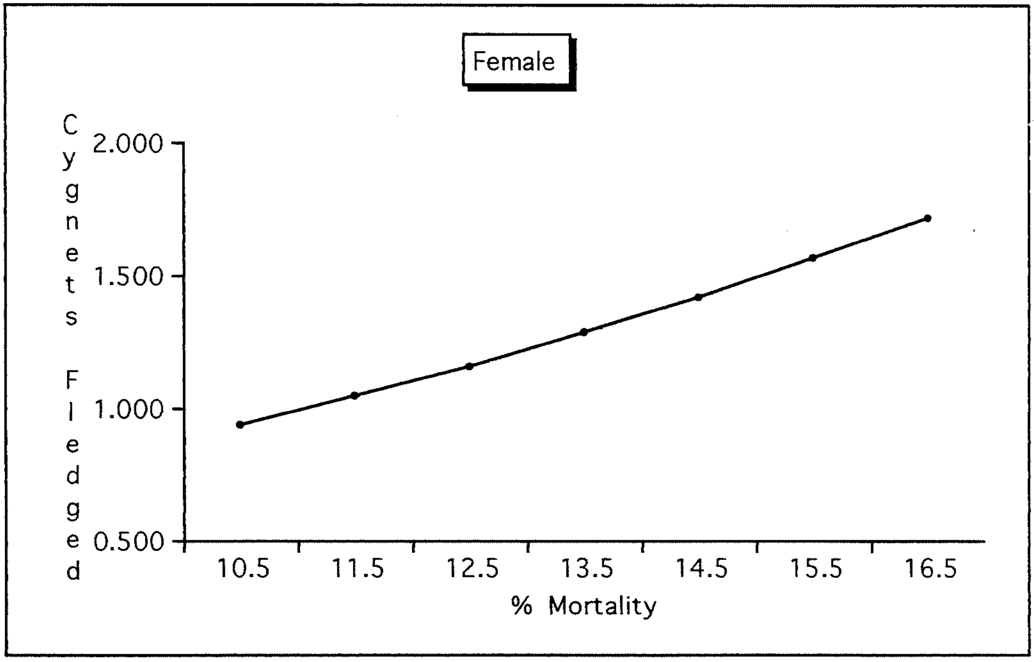


Figure 52. The line of zero change in the number of female breeding swans.

Variation in the proportion of immigrants in the breeding population

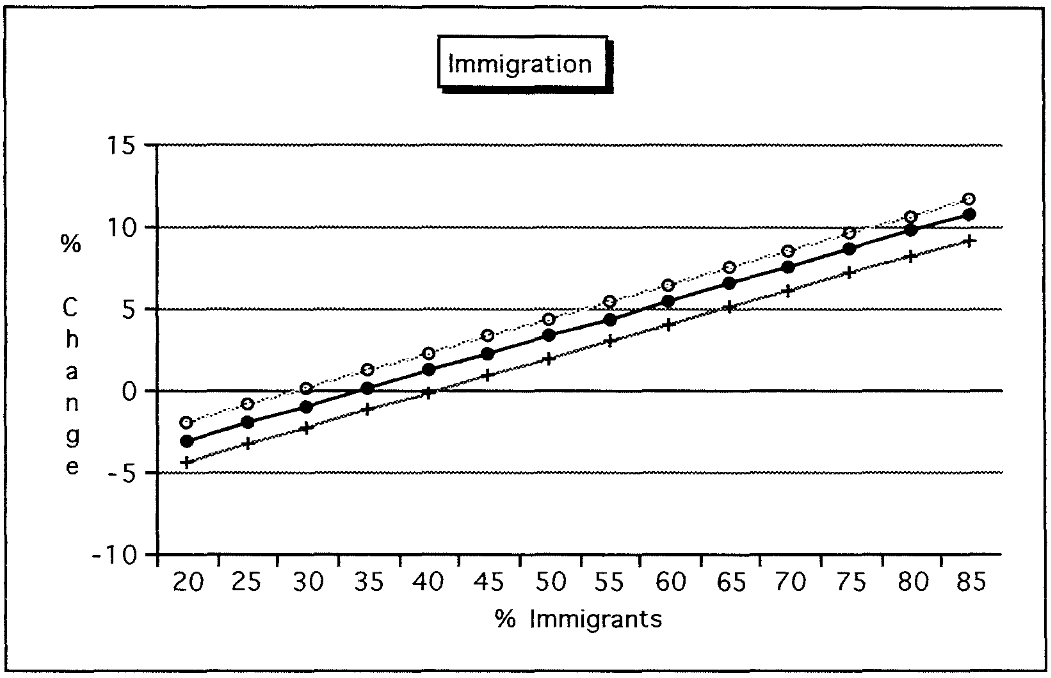


Figure 53. The percentage change which could be expected to occur in the intrinsic segment of the breeding population following a change in proportion of immigrants in the breeding population. Combined sexes (●), males (+) and females (o).

If the proportion of immigrants in the breeding population decreased by more than 11% from the mean, in Model 1, of 45% then the intrinsic portion of the breeding population would have decreased in size (Figure 53). Similarly, the intrinsic male population would have required a greater decrease (20%) and the intrinsic female population would have required only a small decrease (1%) in the proportion of immigrants in their respective breeding populations before a decline in their numbers occurred.

Substantial increases would have been necessary to achieve a 9% annual increase in the intrinsic breeding populations. This would have been achieved if the proportion of immigrants for combined sexes exceeded 73%, the proportion of male immigrants exceeded 84% and the proportion of female immigrants exceeded 72%.

Variation in the proportion of swans which temporarily left the breeding population

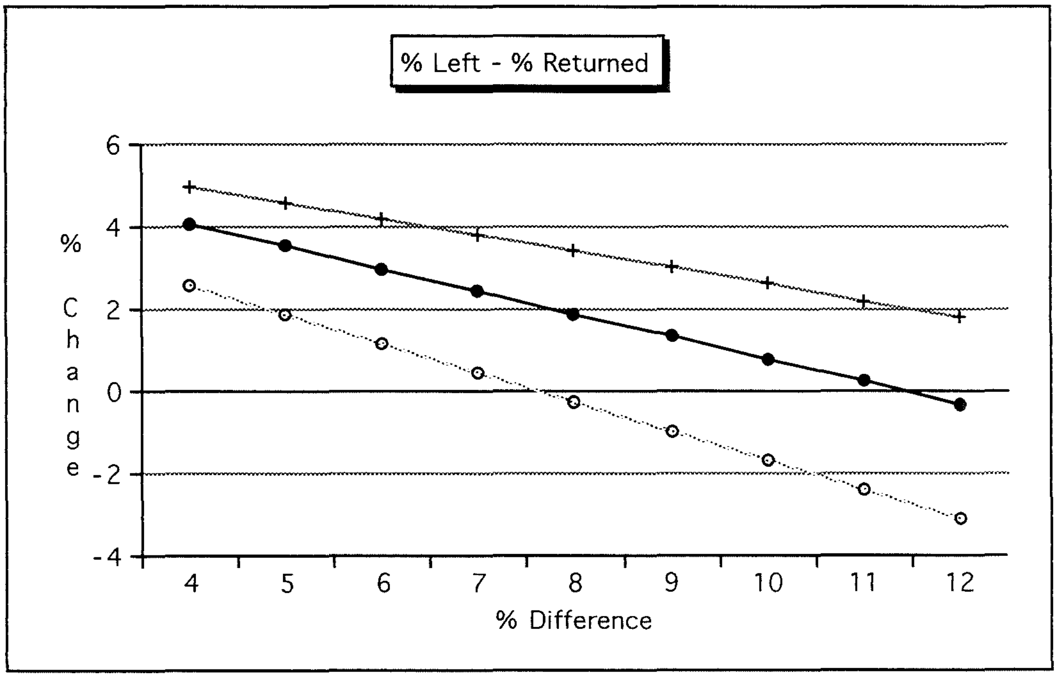


Figure 54. The effect of variation in the percentage of swans which temporarily left the breeding population, combined sexes (●), males (+) and females (o).

The difference between the percentage of the breeding population which left and the percentage which returned was found to average 7.1% per annum for combined sexes, 5.8%

for males and 7.4% for females. A decrease in this parameter could not have accounted alone for a 9% annual increase in the breeding population. However, if the value for combined sexes increased beyond 11.5% (and all other parameters remained unchanged) then a decrease in the intrinsic segment of the breeding population would have resulted. The similar value for males was 16.7% and for females 7.6%. Although this parameter involved only a small proportion of the breeding population it had the potential to cause a decline in the intrinsic segment of the breeding population.

Variation in the percentage of swans which emigrated or never bred

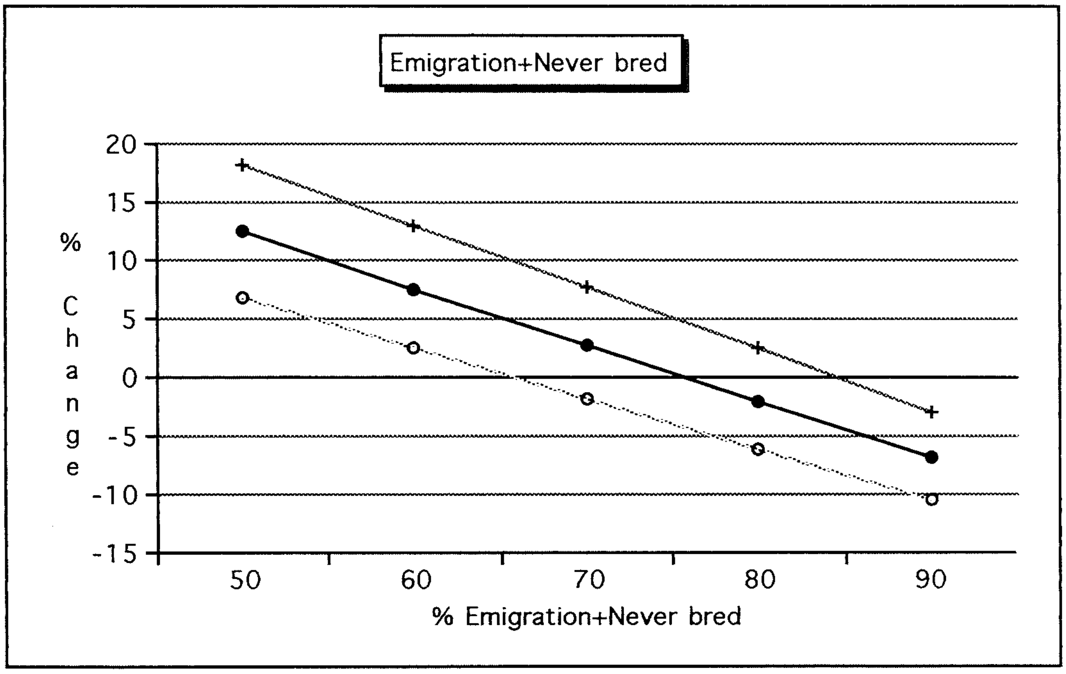


Figure 55. The changes which could occur in the intrinsic segment of the breeding population due to variation in the percentage of swans which hatched in the Lothians and survived to breeding age but emigrated or never bred. Combined sexes (●), males (+) and females (o).

A decrease in the level of emigration plus birds which never bred of 14% from the mean of 71% would have accounted for a 9% increase in the intrinsic segment of the breeding population. However, an increase of just 5% would have resulted in a decline in the number of breeding birds. A 9% decrease from the mean of 77% for males would have accounted for a 9% increase in the intrinsic segment of breeding males while an 8% increase would have resulted in a decline. A large decrease of 20% would have been required in the female segment in order to achieve a 9% increase and a decline in breeding numbers would have resulted from any increase in emigration.

Variation in the age at first breeding

Swans bred for the first time in the Lothians from the age of 2 years to the age of 7 years. By moving the age specific proportions of birds breeding for the first time forward by one year from 3 years to 8 years, forward by two years from 4 years to 9 years or back by one year from 1 year to 6 years it was possible to determine the percentage change which might occur in the intrinsic portion of the breeding population if the age at first breeding varied.

If mean mortality in the breeding population remained at 14.3% then an increase in the age of first breeding would have caused a decline in the intrinsic portion of the breeding population (Figure 56). However, there would have been no change in the intrinsic portion of the breeding population if a one year increase in the age at first breeding occurred in conjunction with a 1% decrease in mortality (and in post-fledging mortality).

Since a proportion of swans commenced breeding at the age of two years it was possible to move the age at first breeding back by one year only. Such a move was insufficient to account for a 9% increase in the breeding population, this would have required a 4% decrease in mortality also.

It was likely that if the age at first breeding changed then the number of age classes in the age range might have varied, as might the proportion of swans in each age class. Consequently, the effect of a change in the age of first breeding on the change which could occur in the intrinsic segment of the breeding population could be greater than indicated above.

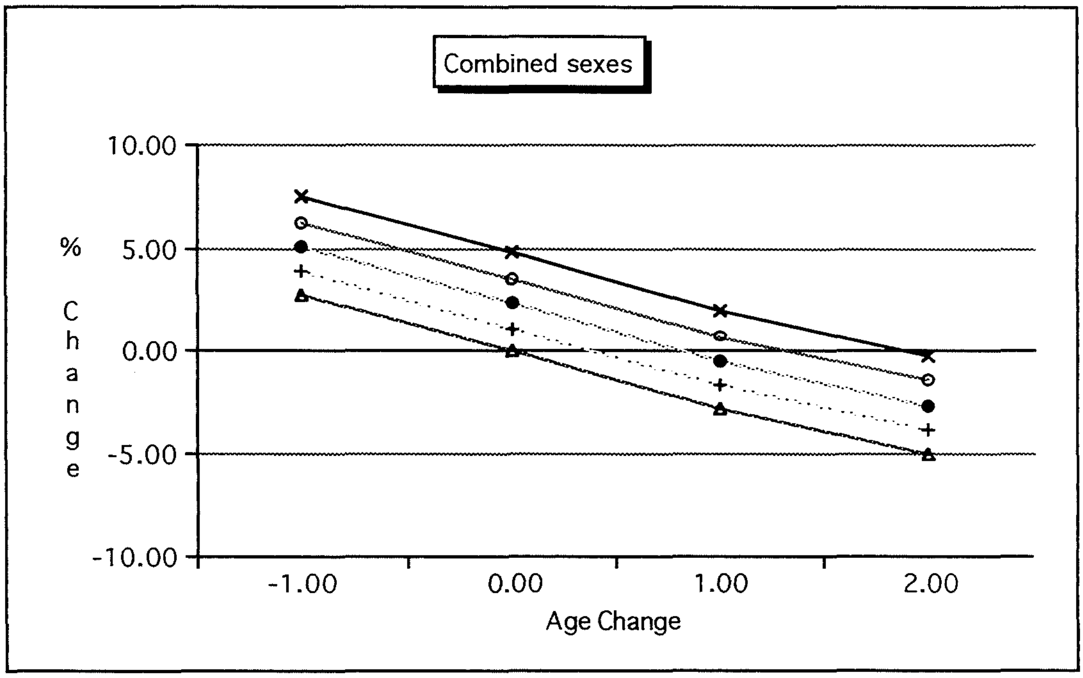


Figure 56. The changes which could occur in the intrinsic segment of the breeding population if the age at which swans bred for the first time changed and mortality changed by +2% (x), +1% (o), 0% (●), -1% (+) and -2% (△).

The male population could have tolerated an increase in the age at first breeding of 1% but not a 2% increase, if all other parameters remained unchanged (Figure 57). If an increase of more than one year occurred then a decrease of 3% in mortality would have been required to prevent a decline in the size of the intrinsic male breeding population.

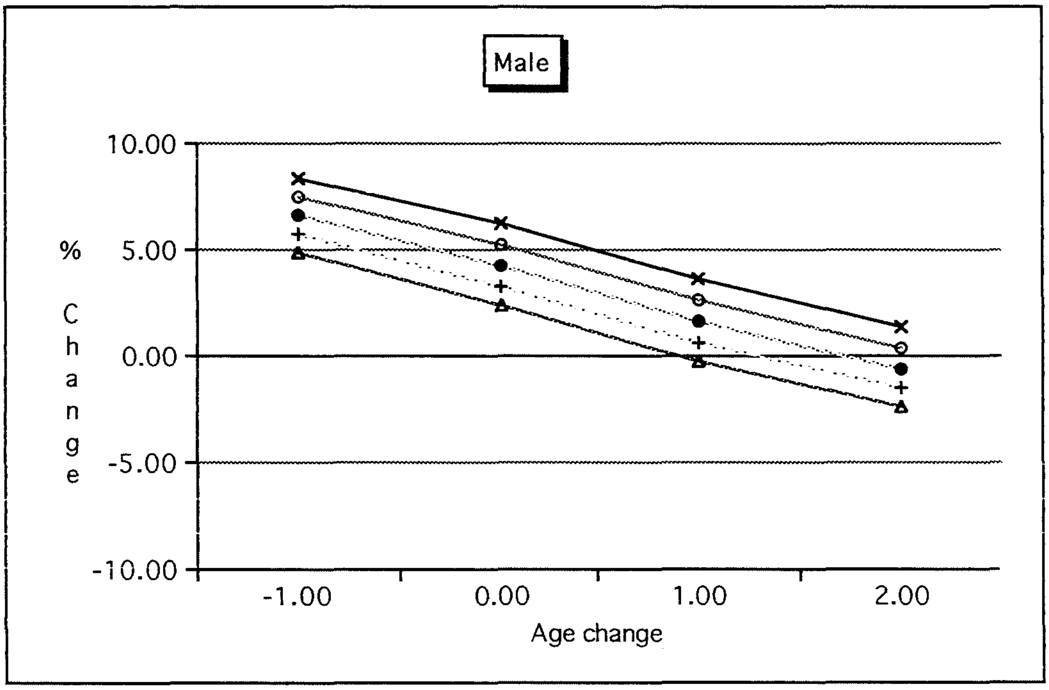


Figure 57. The changes which could occur in the intrinsic segment of the male breeding population if the age at which swans bred for the first time changed and mortality changed by +2% (x), +1% (o), 0% (●), -1% (+) and -2% (Δ).

If the age at which female swans commenced to breed increased then the intrinsic segment of the female breeding population would have declined in numbers (Figure 58). Such a decline could have been averted if mortality decreased also. A larger decrease in mortality of 7% would have been required in addition to a change in the age at first breeding to account for a 9% increase in the intrinsic female population.

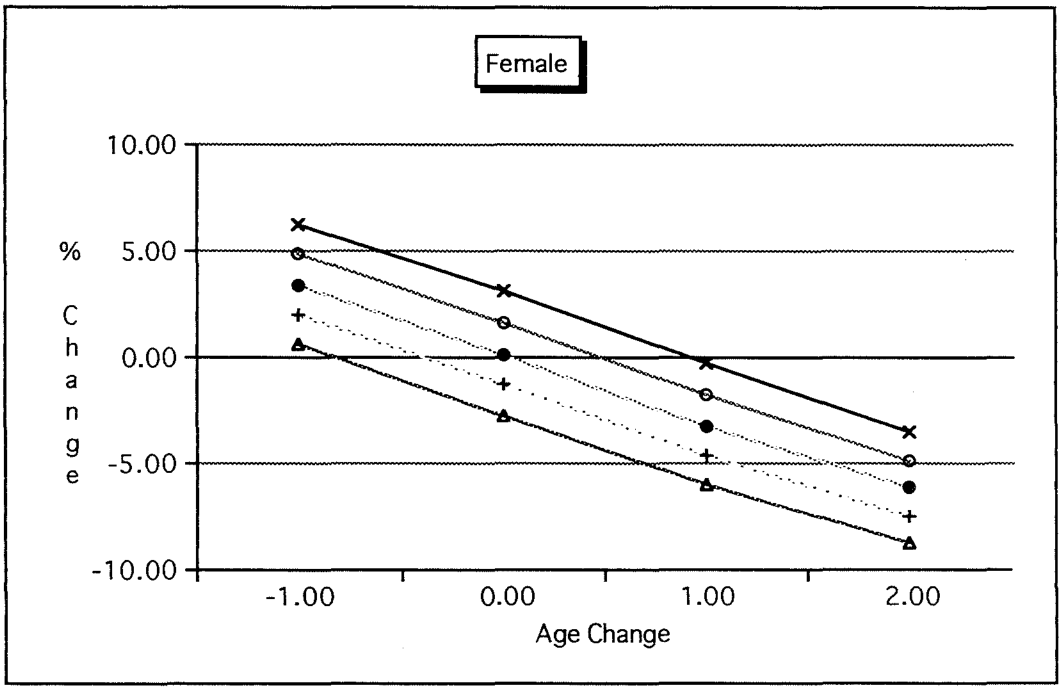


Figure 58. The changes which could occur in the intrinsic segment of the female breeding population if the age at which swans bred for the first time changed and mortality changed by +2% (x), +1% (o), 0% (●), -1% (+) and -2% (Δ).

Discussion

The female intrinsic breeding population in the Lothians could have declined in numbers as a result of a small variation in the estimated mean value for any one of its demographic parameters if the mean values of the remaining parameters remained unchanged. The overall intrinsic breeding population could have coped with a greater variation while the male segment could have tolerated a wide variation in the estimated mean values for many parameters.

Very severe winter weather might have resulted in mortality exceeding 20%, indeed it could have approached 30%. At the other end of the range, mortality might decline to 10% or even lower if favourable conditions prevailed. Similarly, productivity could exceed 3.0 and approach 4.0, while a decline to 1.0 or lower was a feasible possibility. Therefore, no maximum or minimum value could be justified for individual parameters and, given that environmental changes might cause concurrent variations in the value of any number of parameters, then theoretically a large number of permutations in the values of parameters could be anticipated. Consequently, determination of critical values for demographic parameters was not pursued. By continuing to monitor the Mute Swan population in the Lothians it would be possible to detect any change in the mean value for each demographic parameter at an early stage. With the aid of the models it should be possible to anticipate major changes in the population and to avert population declines in exceptional circumstances, for example as occurred in England between the mid 1960's and the early 1980's when approximately 3,000 swans died each year due to lead poisoning (NCC 1981).

Since a number of long-term studies of Mute Swan populations are being conducted in Britain and these studies are fairly widely dispersed in the country it should be possible, through inter study cooperation and implementation of procedures to measure demographic parameters in other areas, to predict major changes in the context of both local and national populations.

Conclusion

The breeding population in the Lothians produced sufficient cygnets to maintain stability in its numbers. Although the population was self-sustaining, it was dependent on immigration to sustain an increase greater than 2% per annum.

Nelson (1978) concluded that no Gannet *Sula bassana* population could maintain an annual increase in excess of 3% from its own productivity and that expansion in excess of 3% was due to immigration. Harris and Wanless (1991) found that the Puffin *Fratercula arctica* population on the Isle of May increased by 19% per annum between 1973 and 1981, the intrinsic rate was 16% and net immigration was 3%. Between 1982 and 1988 the increase was 5% per annum during which time the level of immigration had probably declined. Rapid increases in Gannet *Sula bassana* colonies were shown by Nelson (1978) to have depended on immigration and that as Gannet populations stabilised immigration tended to decline.

Philopatry did not inhibit the number of life-time breeding attempts by philopatric individuals nor, by inference, life-time cygnet production. However, the low level of productivity of such pairs was too low to sustain the breeding population or to contribute to the increase in the number of breeding pairs in the Lothians.

Underlying these findings, however, were different demographies for each gender. In contrast to the male breeding population, the female population was dependent entirely on immigration in order to achieve an increase. The female population demonstrated a greater tendency than the male population to nest close to natal site, this in turn contributed to lower emigration among females than males. Consequently, the intrinsic female population required a greater proportion of recruits to the breeding population than males. These difference were not counteracted by the remaining demographic parameters.

Some breeding territories located within the boundaries of the study area were able to support breeding pairs with reproductive rates in excess of that required to maintain stability in the intrinsic breeding population. The habitat of such territories, where the percentage change in the intrinsic breeding population was positive, has been defined as core habitat (Newton 1989b; Lawton 1996). Habitat which resulted in a reproductive rate insufficient to maintain stability (where the percentage change was negative) in the intrinsic breeding population was designated as sink habitat. Within the Lothians study area, canal habitat and still waters in the mid- and high-altitude habitat categories could be classed as core habitat while river and low altitude still waters could be classed as sink habitat.

Each year a number of breeding territories, both core and sink, remained unoccupied. Many were occupied in previous or subsequent years and the existence of these vacant, but apparently suitable, breeding territories suggested that the number of breeding pairs in the Lothians was not constrained by a lack of breeding territories (it was not a density dependent factor).

The sink population would have depended for its persistence on immigrants from outside the study area and on the excess birds produced by the core population. A proportion of the excess birds from the core population had the opportunity to occupy either sink or core habitat. If they chose to occupy sink habitat then the presence of sink habitat could be perceived as having an inhibiting affect upon the rate of increase of the breeding population. Emigration from the Lothians, and thus immigration in populations outside the Lothians, may have been constrained by the existence of sink habitat in the Lothians. Undoubtedly core and sink habitats were not confined to the Lothians study area and presumably the greater the proportion of sink habitat in a given area the greater the inhibiting effect. This may, in part, account for different population trends recorded from different areas during national censuses and in the change in the proportion of Scottish Mute Swans which occurred in the Lothians.

It is accepted, however, that the classification of still water breeding habitat in three altitude groups was fairly arbitrary as was the classification of river habitat which could, for example, have been subdivided into territories within or outside the tidal zone. The classification of individual breeding territories into core or sink habitat based on productivity of each site would enable calculation of the proportions of core and sink breeding territories in the Lothians.

Data for the Lothians Mute Swan population was sufficient to calculate immigration for the years 1991, 1992 and 1993 when there was a significant increase in the number of breeding swans. The study is on-going and if, in the future, a period of stability or decline occurs in the number of breeding swans it will then be possible to determine whether or not the level of immigration changes with a change in the size of a Mute Swan population.

Critical values could not be determined for each demographic parameter. The number of parameters required to concisely model the demography of a Mute Swan population, combined with the wide range of theoretical values which each parameter might practically justify, resulted in a very large number of permutations of theoretical values for those parameters. Prediction of critical permutations of values for demographic parameters was not undertaken, nor indeed warranted. Any trend towards a decrease in the breeding population could readily be monitored through continued field work. If field work ceased or was reduced in such a way as to reduce the number of quantifiable parameters then any predicted critical permutations could not, in practice, be identified.

Investigations into the balance in the number of birds in other Mute Swan breeding populations have compared productivity with mortality. Immigration and emigration were assumed to be too low to be of any consequence in some studies or too difficult to estimate in others and were, conveniently, disregarded. In addition, all birds which survived to breeding age were presumed to breed with no allowance made for age specific survival to breeding age. Results from the present investigation show that if a realistic determination of a population's ability to sustain its numbers is to be undertaken then all parameters require to be incorporated into that investigation. While immigration and emigration may be irrelevant in the dynamics of truly isolated populations these parameters may be of particular importance in modelling non-isolated populations considered as pests, for example the Cormorant *Phalacrocorax carbo* or even the Ruddy Duck *Oxyura jamaicensis*. Small errors in the calculation of immigration in the Lothians Mute Swan population could lead a large error in estimated size of change in the population, thus such estimates must always be treated with caution. While the number of birds which bred in one year but not in subsequent years may have relatively little effect on the Lothians Mute Swan population it might well have a large impact on endangered species, in addition to endemic or island population which are numerically small. Inaccurate estimations derived from models, or even the disregard of any parameter in a population viability assessment model, may lead to population extinction in endangered species if such a model formed the basis of species management procedures.

The detailed study of habitat use formed the basis of conservation biology in earlier years but is now considered labour intensive (slow and expensive) and not suited to wider generalisations. Community theories, which predominate at present, may be more widely applied but place less emphasis on field work and greater emphasis on theoretical modelling and the inherent danger is that if the models are flawed then their application by land managers may be destructive rather than constructive. Metapopulation theory which includes the concept of core and sink populations is one such community theory, however, is largely untested since there are few long term studies upon which it may be tried. Data collected from the long term study of the Mute Swan population in the Lothians offers the opportunity to investigate metapopulation theory and therefore make a substantial contribution the understanding of population dynamics. Indeed, the value of the study may be enhanced by its potential to test metapopulation theory on individual genders within the population.

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Appendix 1

A copy of the recording form for non-territorial swan data

MUTE SWAN RECORDS - THE LOTHIANS

YEAR:

Observer:

Site:

Grid Ref:

N.B. Note breeding data on separate breeding form

DATE	OBSERVATIONS[1]	COMMENTS

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1. Please record as many counts as possible throughout the year but especially undertake non-breeding counts in mid-APRIL and moulting counts, including failed breeders, in JULY/AUGUST. Distinguish adults and juvs/immatures if possible and note any colour rings and other information in comments column.

Please return completed forms to us as soon as possible after the end of January; if more than one form is used per site then forms could be sent earlier, especially if colour-ringing information is recorded.

A.W. & L.M.Brown.
61, WATT'S GARDENS
CUPAR,
FIFE KY15 4UG Tel: 0334-56806

Appendix 2.

A copy of the recording form for territorial swan data

MUTE SWAN BREEDING CENSUS - THE LOTHIANS **YEAR:**

Observer:

Site:

Nest Location:

Grid Ref:

N.B. Please use ONE form per breeding pair

DATE	OBSERVATIONS[1]								COMMENTS
	T	N	C	H	S	L	F	CR	

[1] T=pair in territory(from mid-March),N=pair with nest(if present regular visits should be made until y.hatch or pairs fail),C=clutch size if known,H=no.of cygnets hatched,S=no.of small young,L=no.of large young,F=no.of fledged young,usually by mid-Sept. Indicate reasons for failure,if known, in comments column and any other relevant information. CR=note and record any colour-ringed adults.

Please return completed forms to us by end of October but advise of progress of broods so that preparations can be made for ringing in August.

A.W. & L.M.Brown.
61, WATT'S GARDENS
CUPAR,
FIFE, KY15 4UG   Tel: 0334-56804

Appendix 3.

The "break-point" at 1985 was determined by "Broken Stick" Analysis using regression facility in the Minitab 10 statistical package. Regression models of the form :-

$$E[y] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$$

were fitted where the dependent variable, y, was the total population and the independent variables were :-

x_1 , the year (with 1978-1993 coded 1-16).

x_2 , a dummy variable taking the value 0 for the years in the early period, 1978-1985, and the value 1 for the years in the late period, 1986-1993.

x_3 , the product of x_1 and x_2.

The model is equivalent to the two straight line models :-

$E[y] = \beta_0 + \beta_1 x_1$ early period

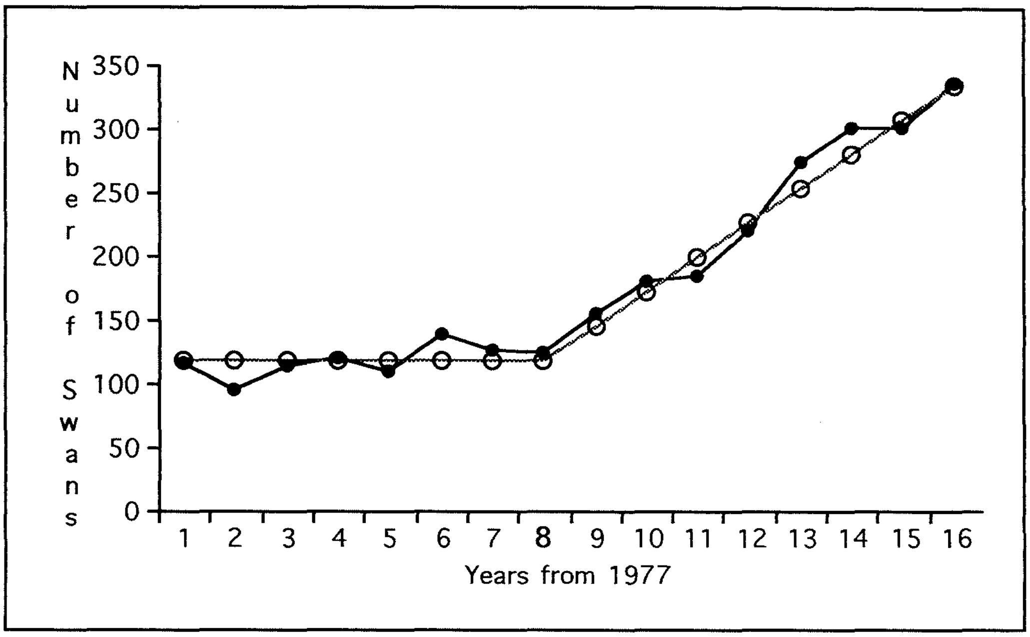
$E[y] = (\beta_0 + \beta_2) + (\beta_1 + \beta_2) x_1$ late period

The initial model, with the break-point at 1985, yielded an estimate of β_1 which did not differ significantly from zero so the term in x_1 was excluded from the model. The final model, with rounded coefficients, was equivalent to :-

$E[y] = 119$ early period

$E[y] = -87+27x_1$ late period

This indicates an expected constant total population of 119 during the early period from 1978 to 1985 and an expected increase of 27 swans per year from 1986 to 1993. The R^2 value of 97.6% indicated that 97.6% of the variation in y was explained. The fitted model is shown below.



The Total Population (●) of Mute Swans in the Lothians in April and the Fitted Model (O) of the total population.

Further analysis indicated that an earlier break-point than 1985 yielded an early period with a constant total population and a late period with an upward trend in the total population. Since it emerged also that break-points later than 1985 gave rise to upward trends in both periods, then 1985 was the latest break-point to give a period of stability followed by a period with an upward trend. Consequently the break-point was taken at 1985 in order to compare a period of stability in the swan population (1978-1985) with a period of increase (1986-1993). This decision was supported by an analysis of the data (after differentiating) carried out using the test proposed by A.N. Pettitt (1979) for the detection of a change in a sequence of random variables (James Forster) pers. comm.

Appendix 4

The number of cygnets fledged by each breeding pair from 1981 to 1993.

	Number of cygnets per breeding pair		
Year	River	Canal	Still water
1981	2, 1, 5, 6, 0, 0, 0	5	5, 4, 4, 7, 6, 2, 8, 3, 6, 6, 2, 0, 0, 0, 0, 0, 0, 0
1982	3, 3, 5, 6, 6, 0, 0	0	3, 4, 1, 9, 2, 3, 8, 3, 8, 7, 4, 0, 0, 0, 0, 0, 0, 0
1983	6, 4, 0, 0, 0, 0, 0, 0	0	3, 2, 7, 5, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
1984	4, 5, 3, 4, 0, 0, 0	1, 4, 0	1, 7, 6, 1, 8, 5, 7, 3, 4, 4, 0, 0, 0, 0, 0, 0, 0, 0
1985	6, 5, 3, 3, 5, 0, 0	1, 6	4, 8, 1, 2, 7, 4, 5, 6, 4, 3, 7, 3, 8
1986	6, 4, 6, 4, 6, 0, 0	1, 5, 3	4, 3, 3, 2, 3, 6, 4, 2, 2, 4, 0, 0, 0, 0, 0, 0, 0, 0, 0
1987	2, 6, 1, 4, 10, 0	2, 7, 5, 0	8, 6, 5, 2, 9, 4, 4, 8, 5, 5, 2, 1, 2, 4, 4, 0, 0, 0, 0, 0, 0, 0
1988	4, 5, 4, 0, 0, 0, 0, 0, 0	2, 4, 6, 0	7, 6, 8, 5, 3, 6, 5, 5, 7, 1, 4, 4, 2, 7, 7, 2, 6, 0, 0, 0, 0
1989	2, 8, 1, 3, 6, 0, 0, 0, 0, 0, 0, 0	4, 7	6, 5, 4, 4, 7, 3, 8, 8, 2, 4, 3, 8, 8, 5, 1, 2, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
1990	4, 1, 6, 1, 5, 4, 0, 0, 0	5, 6, 4, 3, 7, 0, 0	1, 9, 8, 4, 3, 4, 3, 3, 5, 6, 6, 9, 4, 5, 5, 1, 1, 2, 5, 2, 5, 2, 0, 0, 0, 0, 0, 0, 0
1991	1, 3, 2, 4, 2, 2, 0, 0	6, 8, 4, 3, 6, 0	5, 9, 1, 3, 4, 3, 4, 6, 4, 2, 2, 1, 1, 4, 9, 6, 4, 3, 6, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
1992	1, 2, 2, 2, 0, 0, 0, 0, 0, 0, 0, 0, 0	8, 8, 5, 4, 7, 5, 0, 0	4, 1, 3, 7, 4, 1, 6, 3, 5, 7, 9, 4, 1, 7, 4, 4, 4, 5, 5, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
1993	3, 4, 3, 0, 0, 0, 0, 0	7, 1, 1, 4, 7, 0, 0, 0, 0	6, 4, 3, 1, 8, 1, 4, 4, 3, 2, 3, 5, 5, 3, 3, 3, 8, 8, 6, 1, 6, 4, 4, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0

Appendix 5

The number of cygnets fledged per breeding pair in each altitudinal category of still waters.

Altitudinal category	Number of cygnets per breeding pair
0-50m	3, 0, 1, 0, 4, 0, 6, 0, 9, 5, 1, 0, 0, 1, 0, 0, 1, 0, 0, 3, 0, 4, 3, 7, 4, 2, 0, 0, 1, 7, 0, 3, 0, 8, 7, 3, 0, 2, 0, 1, 4, 0, 2, 0, 3, 0, 5, 4, 0, 6, 3, 0, 1, 0, 6, 8, 0, 8, 5, 0, 4, 5, 0, 0, 0, 0, 0, 2, 3, 0, 0, 6, 3, 4, 0, 6, 6, 5, 4, 0, 0, 0, 0, 0, 1, 0, 3, 6, 5, 0, 7, 3, 7, 3, 4, 2, 0, 5, 2, 4, 4, 4, 0, 5, 5, 0, 2, 1, 1, 1, 0, 0, 0, 0, 4, 0, 0, 0, 0, 0, 0, 3, 2, 0, 0, 0, 0, 0, 2, 0, 2, 3, 1, 0, 1, 5, 0, 0, 0, 3, 0, 0, 0, 7, 2, 4, 0, 0, 0, 0, 0, 3, 5, 1, 0, 6, 0, 0, 5, 0, 0, 0, 4, 4, 7, 6, 1, 0, 4, 6, 0, 0
51-100m	5, 4, 3, 1, 3, 0, 7, 0, 2, 6, 4, 3, 4, 0, 4, 3, 8, 8, 7, 5, 4, 6, 8, 6, 8, 9, 2, 7, 3, 6, 7, 2, 4, 2, 9, 4, 4, 6
101-270m	4, 4, 0, 7, 8, 3, 8, 5, 0, 8, 5, 8, 9, 0, 6, 3, 5, 0, 0, 4, 0, 0, 0, 0, 0, 4, 9, 6, 2, 0, 0, 3, 1, 1, 8, 6, 0, 4, 4, 3, 0, 3, 6, 0, 7, 1, 4, 4, 0, 9, 7, 2, 8, 8, 5, 1, 5, 0, 2, 0, 9, 0, 7, 4, 8, 3, 5, 6, 4, 8, 2, 4, 0, 4, 8, 0, 4, 0, 6, 0, 2, 0, 0, 0, 5, 4, 0, 0, 3, 0, 2