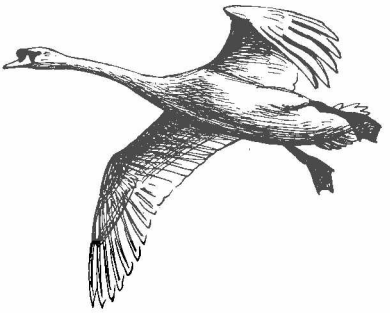
A study of the breeding Mute Swans *Cygnus olor* at Abbotsbury



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The breeding population has varied between 18 and 130 pairs, with an increasing proportion of the breeding birds having themselves been raised in the colony. The age of first breeding is similar to that in other studies in the UK, but clutch-size is smaller and annual survival rates more variable. The number of breeding pairs is very sensitive to the over-winter adult survival rate, falling when survival is low, rising when it is high. The ages of the two members of each pair are closely correlated, even though the birds may have several mates during their life-times.

Keywords: Mute Swan, Breeding Age, Breeding Success, Survival Age of Partner

The Abbotsbury Swannery is famous as being the only well-established colony of Mute Swans *Cygnus olor* in the British Isles (for a general description see Perrins & Ogilvie 1981). During 1993 the Ilchester Estate, the owner of the Swannery, celebrated the 600th anniversary of the earliest recorded statement about the swannery (Fair & Moxom 1993). This indicated that the methods of managing the colony were well-established by 1393 and so the colony must be of even older origin. The study started in the late 1960s, but the breeding birds in the colony were not marked consistently until 1977.

The Swannery is situated at the west end of the Fleet, a 14 km long stretch of water which lies behind the Chesil Bank in Dorset. The Fleet opens to the sea at the eastern end; it is therefore tidal and the water is salt at the eastern end with the salinity gradually falling towards the western end where the water is almost fresh. A large number of Mute Swans live on the Fleet, others move in to moult in late summer or to winter (Perrins & Ogilvie 1981). During the years of the study, from 18 to 130 pairs have attempted to breed. The large majority of these nest within the central area of the colony, each within two to twenty metres of the next nearest pair. A few are concealed from view of other nests and one or two are outliers, several hundred metres from the colony itself, though still much closer than one would normally find on open waters elsewhere. Almost no nesting attempts are made outside the Swannery Bay at the west of the Fleet; the outliers usually fail to raise any young.

The study reported here was carried out jointly by members of the Edward Grey Institute and The Wildfowl and Wetlands Trust, with much of the field recording being done by staff at the Swannery. In this paper, we examine the origins and some of the attributes of the breeding birds in the colony.

Methods

One of the features of the Swannery is the rearing pens where cygnets, often from several broods, are placed with a single pair of parents. In the early years of the study few cygnets survived other than those reared in the pens. In recent years, the situation has changed; with increased care, more of the cygnets now survive and, in 1993, only about one-third of the surviving cygnets were raised in the pens. However, because many of the chicks are taken from their parents and raised in pens, and also because cygnets often end up in a brood other than their true one, we have not examined the breeding success of the individual pairs beyond the point of hatching.

The nests are visited by the Swannery staff on a regular basis, in recent years twice daily during the laying and hatching periods. Virtually all of the breeding adults are already ringed with large, numbered plastic rings, so that identification is not a problem. Some difficulties arise at some

nests by one or other of the pair being absent on all visits and so not identified; at a few nests which fail, this may result in one (or both) member(s) of the pair not being identified. But, at nests which hatch young we know the identities of virtually all the parent birds. Some problems occasionally arise with regard to the sex of parents which is usually determined by looking at the relative sizes of the members of the pair (using characteristics such as overall size, knob size and size of the feet). Discrepancies that arise in the recorded sex of the breeding birds between years can usually be resolved from the records or, in birds which were born in the colony in or after 1977, from records of the sex of the birds at ringing or, in recent years, at hatching. Occasionally, the same male is recorded as being the parent at two adjacent nests; we cannot be certain whether this is genuine or arises from one of two males being dominant around the nests and preventing the other from visiting for much of the time; we have no information on the parentage of the cygnets from such nests.

All the cygnets raised at the Swannery are marked with a tiny, but distinctive nick in the web. Hence we have been able to recognise Abbotsbury-born cygnets, even those born in the years before the study began, with almost 100% certainty. Since 1976 almost all the cygnets have been ringed in September.

The number of nests recorded is the number of nests in which at least one egg was laid. The building of a nest cannot be easily recorded since the Swannery staff make some initial piles of reeds for the birds and some birds do not seem to add greatly to these. A small number of nests may never progress beyond the one-egg stage and the parents of such nests are often not identified. We cannot therefore be certain that these nests are genuine attempts by an unrecorded pair rather than egg-dumping or repeat clutches from already recorded pairs (these incomplete clutches are often produced late in the season). We have almost no information on possible egg-dumping though, since the Mute Swan normally lays its eggs at two-day intervals and there are (very rare) records of eggs appearing in nests at 24 hour intervals, some egg-dumping must occur. However, its incidence is clearly very low.

There are problems with statistical testing on many of the data. Because the Mute

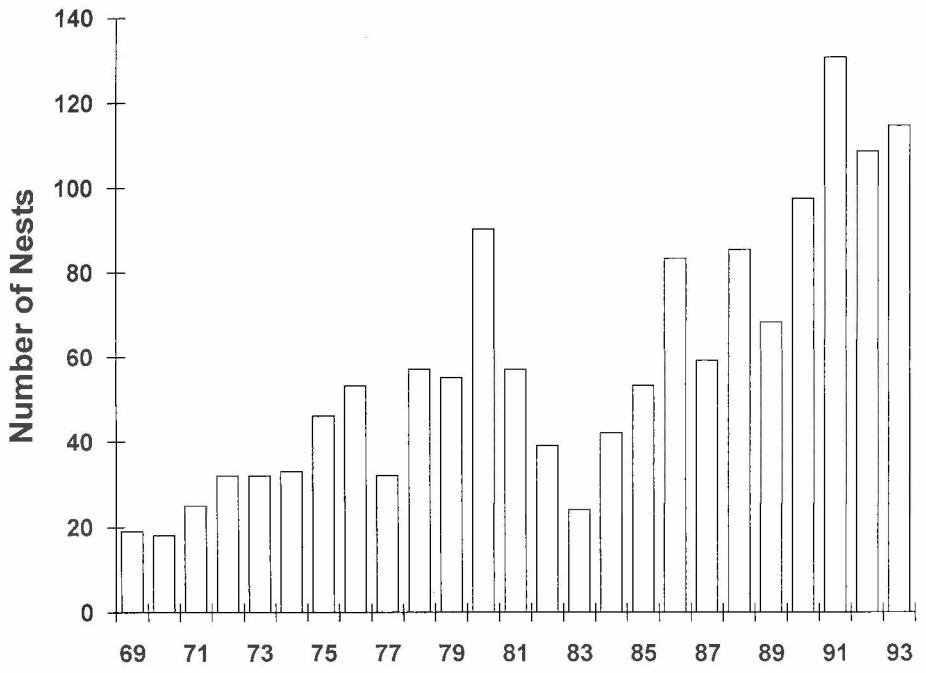

Figure 1. The number of nesting pairs of Mute Swans in the Abbotsbury colony 1969-93. The numbers include a few outliers which nest almost territorially.

Swan is a relatively long-lived bird, many individuals contribute to the data points in several successive years. Hence these data are not, strictly speaking, independent and it is not always easy to allow for this.

Results

Number of Breeding Pairs

Figure 1 shows the number of clutches started each year at the Swannery. There are two points to note. First, there has been a gradual increase in the numbers breeding with time (the highest numbers in recent years compare favourably with the highest ever recorded, this being 130 in 1885). One possible reason for this increase is that in 1974 the management changed, resulting in larger numbers of cygnets being produced per year. Since the locally born cygnets form a major component of the breeding population, this has probably led, at least in part, to the recent increase in breeding pairs. Second, the decreases in numbers are almost certainly associated mainly with bad winters and lowered survival as discussed below; in this respect it is worth noting that in the early part of 1982 there was a particularly severe spell of weather which probably lead to the low survival from 1981-1982. Similarly, Bacon & Andersen-Harild (1989) have shown that the Mute Swans in Danish colonies fare badly in cold winters.

Origins of the breeding birds

Figure 2 shows the percentage of the breeding birds which were raised in the Abbotsbury colony. There are two points to note. First, the proportion of the breeders in the colony which were raised there has increased with time. This is probably a simple reflection of management. As explained above, in 1974 the management of the colony changed, with more food being provided for the cygnets; consequently, these have survived the summer better and left the colony in September at a greater weight than formerly, which probably has increased their chances of surviving the winter. Hence the Fleet probably nowadays houses many more birds raised in the colony than in the earlier years of the study. The second point is that the percentage of Abbotsbury born birds is consistently higher for females than for males (note that since an individual bird breeds in several successive years, the data for the individual years are not independent of

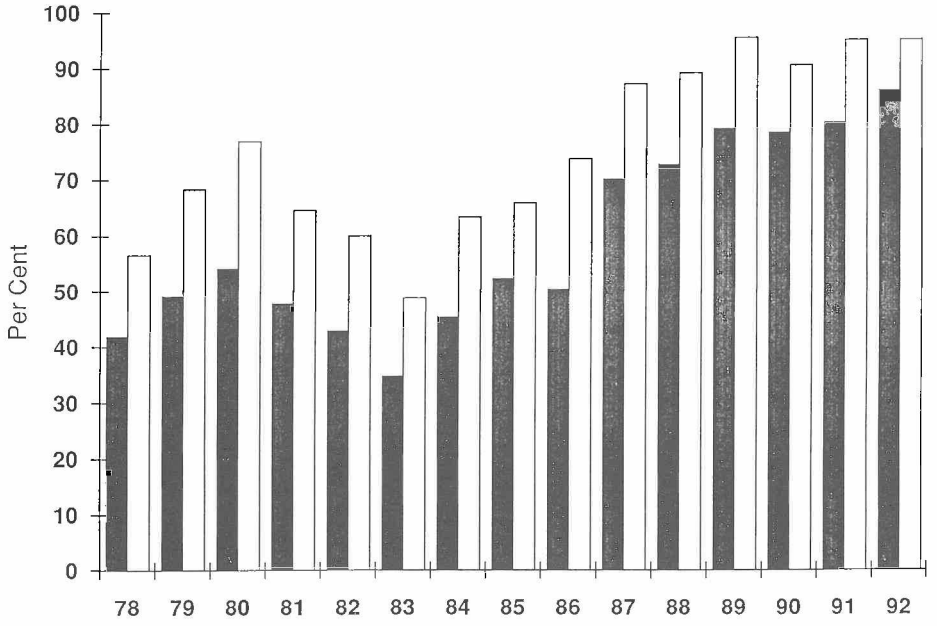

Figure 2. The origins of the Abbotsbury Mute Swan breeders, plotted as a percentage of the breeding birds which were known to have been born at Abbotsbury. Filled column males, open column females.

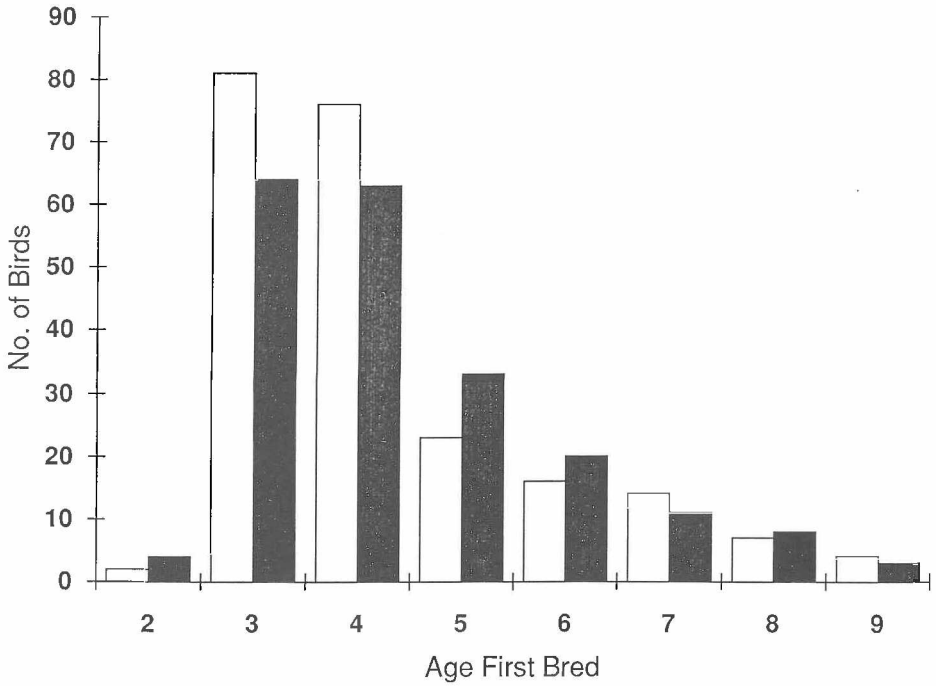

Figure 3. Age at first breeding for Mute Swans breeding in the Abbotsbury colony. Filled columns males, open columns females.

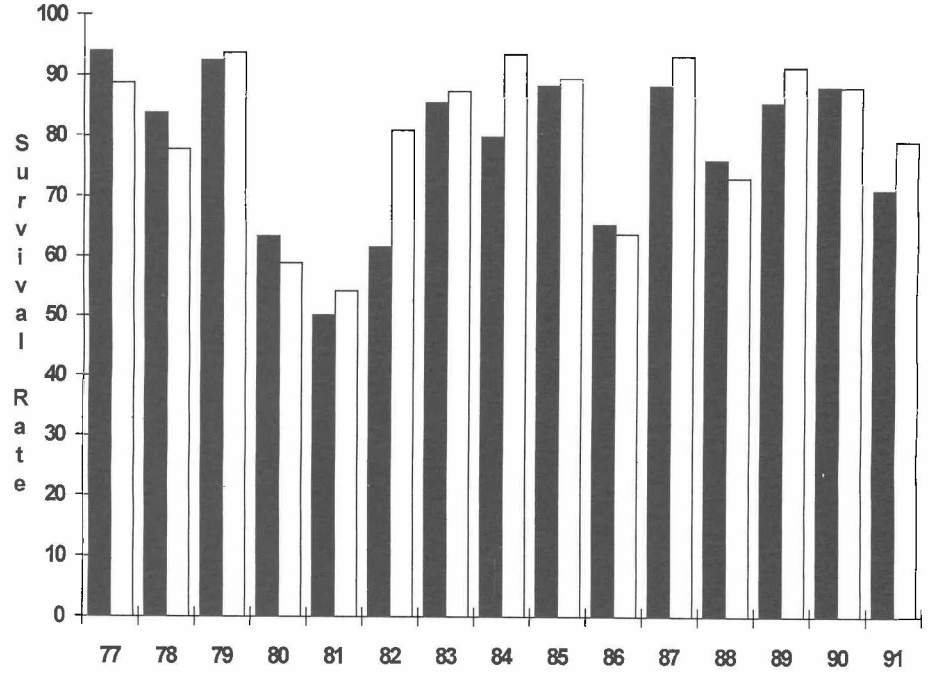

Figure 4. Estimated annual survival rate of breeding Mute Swans at Abbotsbury. Filled columns males, open columns females.

each other). This difference does not seem to arise because more females than males are raised in the colony. It is well-established for several species of wildfowl that the females are more philopatric than the males. It looks as if the same may hold true for the Abbotsbury swans. Presumably it comes about when the Abbotsbury-born birds meet birds born elsewhere (many of which come onto the Fleet in winter); birds are more likely to stay and breed at the swannery if the female member of the pair was born there than if the male was. The corollary would be that there should be more pairs in the surrounding area with Abbotsbury-born males than Abbotsbury-born females, but we do not have enough information to examine this.

Age of First Breeding

Figure 3 shows the age of first breeding of the birds in the colony, based on records for 206 males and 223 females. The data are fairly complete except that, as explained above, some birds which attempted to breed and failed were not identified. Hence we cannot be absolutely certain that some of the birds shown in this figure to have bred for the first time at age eight or nine years had never attempted to breed at an earlier age, though we can be confident that they were not successful breeders at an earlier age.

As with Mute Swans elsewhere in Britain (Birkhead & Perrins 1986), a very small number of birds start to breed at age two and the majority start at either age three or four. Nevertheless, quite a few of the birds do not start breeding until later than this. Over a quarter of the females and about one third of the males do not commence breeding until at least age five. Females start to breed at a slightly earlier age than males with 71.3% of the females breeding by age four, but only 63.6% of the males.

Survival Rates

The survival rates of the breeding birds were calculated using a maximum likelihood model correcting for resighting probability (Clobert *et al.* 1987). Results are plotted in **Figure 4**. The estimated survival rates for the two sexes are shown separately, but there is little difference between them, the mean survival of the breeders

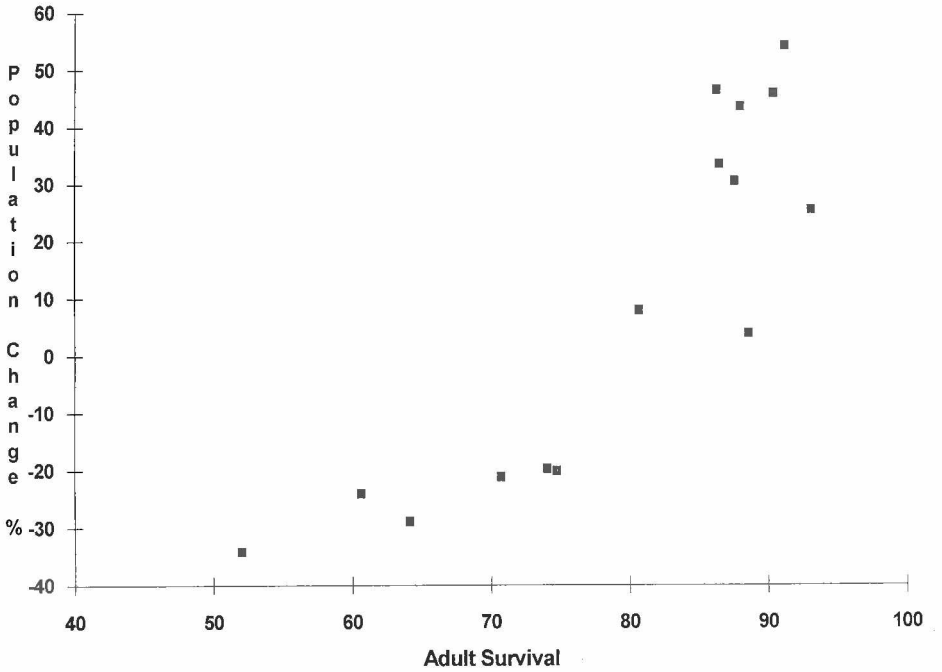

Figure 5. Relationship between annual adult Mute Swan survival rate and population change. Adult survival rate is the mean of the figures of the two sexes (see Fig. 4). Population change is calculated as the percentage change from year t to year t+1. The correlation is highly significant (r^2 = 74.8%, P = <0.001, see text for further explanation).

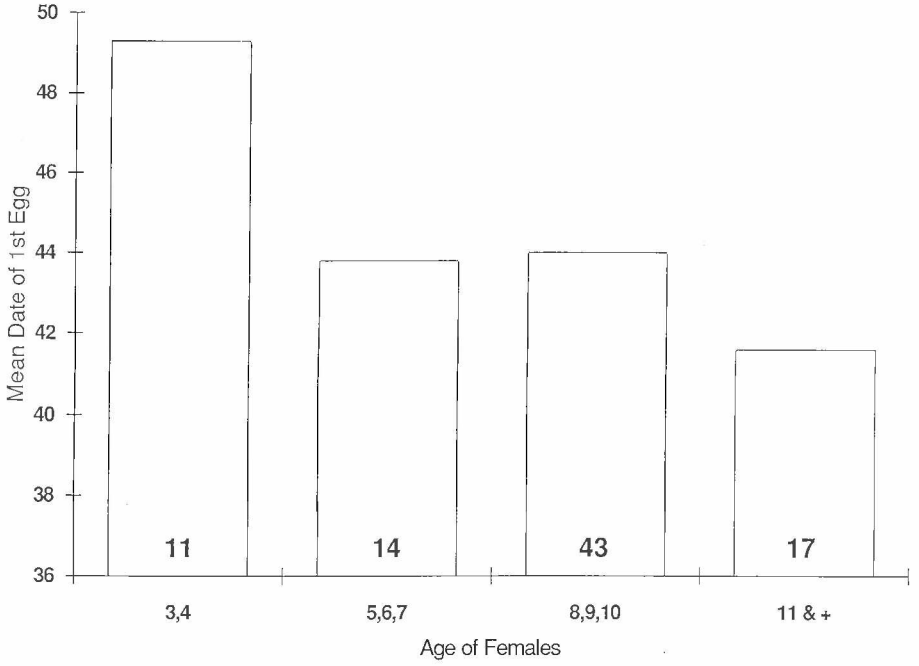

Figure 6. Date of first egg and breeding age of Mute Swans in 1993, grouped as 3-4 years, 5-7 years, 8-10 years and older. Day 1 = 1 March. Numbers in columns are sample sizes.

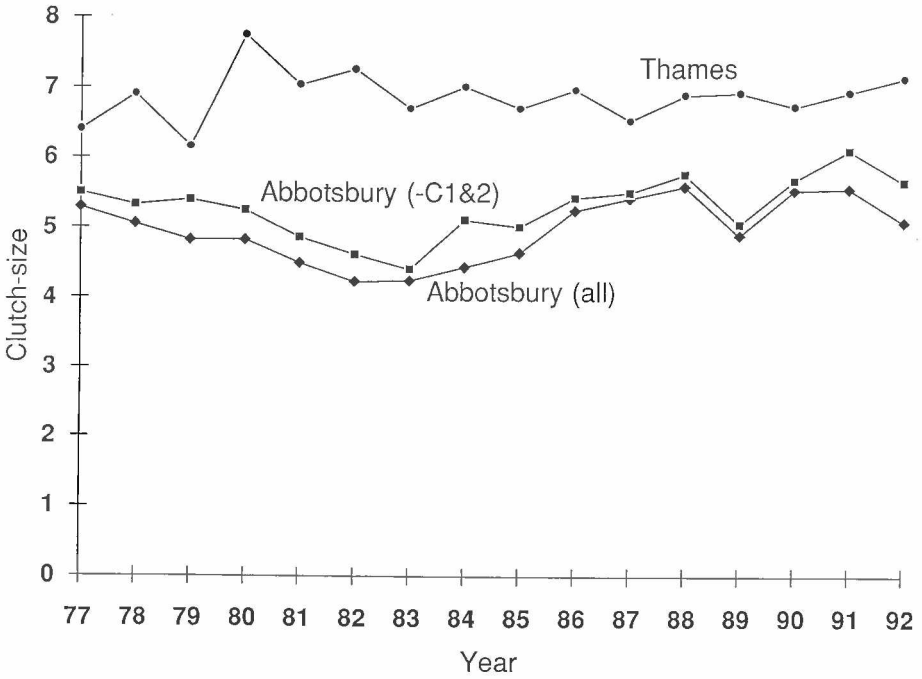

Figure 7. Mean clutch-size of Mute Swans at Abbotsbury compared with that on the River Thames in the same years. Two figures for clutch-size at Abbotsbury are given; the lower one is for all nests started, the higher one excludes all nests where only 1 or 2 eggs were laid. See text for explanation.

from the 15 years 1977-1991 was 77.9% for males and 80.5% for females.

Perrins & Ogilvie (1981) showed the breeding birds at Abbotsbury had a very high survival rate. However, as can be seen from **Figure 4**, with a much longer run of data, this is an oversimplification. Survival rates from one year to the next can be quite high, in some years reaching or exceeding 90%. However, in other years they may be quite low; only 50% of the birds which bred in 1981 survived to the following year.

In years when large numbers of adults die, presumably large numbers of the other birds also die. One would therefore expect that the number of nests the following year would be lower after winters with high mortality of the breeding adults. Another possibility would be that the breeding birds in some way 'excluded' the non-breeders from entering the breeding population in most years and, in the spring following a high mortality of breeders, more of these non-breeders would be able to enter the population and so compensate, at least to some extent, for the loss of the breeders. **Figure 5** plots the change in numbers of breeders against the estimated adult survival during the year from one breeding season to the next. There is a strong positive linear relationship ($F1,13=3.45$, $P=<0.001$) between population change and estimated survival. Inspection of the graph suggests that the relationship may be curved; statistically there is slight evidence for non-linearity (adding a term, survival squared, $F1,12=3.45$, $P=0.088$). This would indicate that, in years with low overwinter survival rates of adults, relatively more recruits enter the population and hence buffer it against even sharper declines in numbers of nests due to the high adult mortality. Further work (Perrins & McCleery in prep) suggests that there is a negative relationship between adult survival and the proportion of the breeding birds which are breeding for the first time.

Breeding parameters

We have information on laying dates, clutch-size and hatching success in the population though not (for the reasons explained above) information on fledging success of the individual pairs.

i) Laying date

Figure 6 shows the laying date for the birds that bred in 1993. The older birds laid significantly earlier than those breeding at ages of three or four. In these data, the birds that bred at ages of five to ten were intermediate between the others, but showed no evidence of laying progressively earlier within these ages.

ii) Clutch-size

The clutch-size of the birds laid at Abbotsbury seems to be small in comparison with published figures for Mute Swans elsewhere in Britain. One difficulty is that recording methods differ between Abbotsbury and other studies. In most studies, because the nests are far apart, it is not possible to visit the nests on a daily basis. Hence there is the chance that some nests which are started, and in which just one or two eggs are laid, and are then deserted or predated, will be missed. Such under-recording of these small, and possibly incomplete, clutches will result in an increase in the apparent mean clutch for such populations. At Abbotsbury however, the nests are visited on a daily basis and so such nests are found and recorded.

Nevertheless, the small mean clutch at Abbotsbury seems genuine. **Figure 7** shows the mean clutch for the Thames area, based on the Oxford study (Bacon & Perrins 1991, Lievesley in prep.) and the data from Abbotsbury for the same years. The latter is plotted in two ways, first including all the very small (and usually presumably incomplete) clutches and second, after excluding all the one or two egg "clutches". The mean clutch at Abbotsbury is always at least one egg and sometimes more than two eggs smaller than that on the Thames.

In several studies there has been a decline in clutch-size during the breeding season (Reynolds 1972, Bacon 1980); such a decline seems to be present at Abbotsbury, but is not very marked, possibly because of the lowered overall clutch-size.

Figure 8 shows the mean clutch-sizes of the birds in relation to age. Data for all years have been lumped together, so many birds contribute several data points to this figure. Clutch-size increases with age up until about the age of ten, after which it levels off. In the very small number of birds of age 14 or more, clutch-size is slightly lower suggesting that reproductive output may decline in the oldest age groups.

iii) Hatching Success

Figure 9 shows the hatching success of the

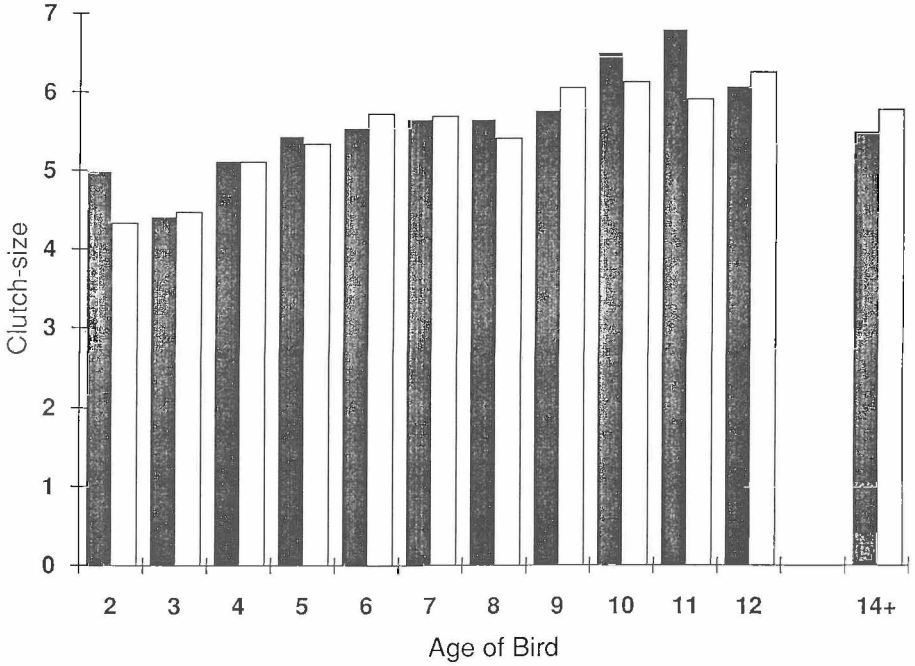

Figure 8. Clutch-size and age of parent Mute Swans. Filled columns males, open columns females.

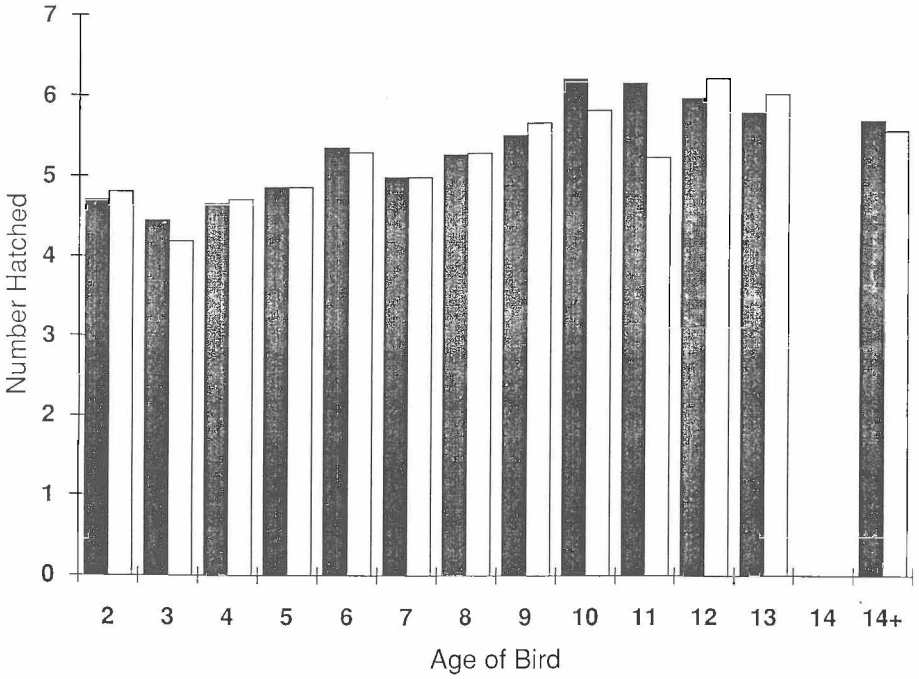

Figure 9. Number hatched and age of parent Mute Swans. Filled columns males, open columns females.

birds in relation to age. As with the data for clutch-size, many birds contribute several data to this figure; again, hatching success increases with age and perhaps declines in the oldest age groups.

The reason for the similarity of this pattern to that of clutch-size is that the number hatched is largely dependent on clutch-size. However, there is some slight evidence that the age effects of hatching success are more marked than those of clutch-size. This is because the older birds seem more likely to hatch their clutch than the younger ones. **Figure 10** shows the mean age of birds which a) fail to hatch any young at all and b) which hatched at least one cygnet. For both sexes, the average age of the successful birds is higher than that of the unsuccessful ones, though in neither sex is the difference statistically significant.

Age of Partners within a Pair

Figure 8 showed clutch-size in relation to age for males and females separately, even though only females lay eggs! Yet, as with the females, there is a close correlation between clutch-size and the age of the males. There are two possible explanations for this. First, the clutch-size of the female might related in some way to the efficiency (and hence the age) of her partner; this could come about, for example, if the male guarded the female during the time when she was feeding to get into good condition for egg-laying as happens with the Shelduck *Tadorna tadorna* (Patterson 1982) and probably in some geese where condition affects clutch-size (Ankney & MacInnes 1978, Drent & Daan 1979). Alternatively, the ages of the males and the females may be correlated with the choice of partners of the same age (Minton 1967).

In the case of the Abbotsbury swans, there does not seem to be much evidence for the first of these possibilities. Although the data are few, comparing females of the same age who have mates of different ages, their clutch-size does not seem to vary with the age of the mate. The reason why there are few data is that there is a very strong tendency for each swan to be mated to another of a similar age (**Figure 11**). In order to avoid the problem that a pair of birds might contribute a series of data points to this sample, we have used, in this analysis, only the ages of each pair when they mated together for the first time. Thus, if it paired with several mates, a bird might contribute several data points to this analysis, but only one with each mate. **Figure 11** is based on the ages of the birds in 208 first-time pairings.

There is another reason why a correla-

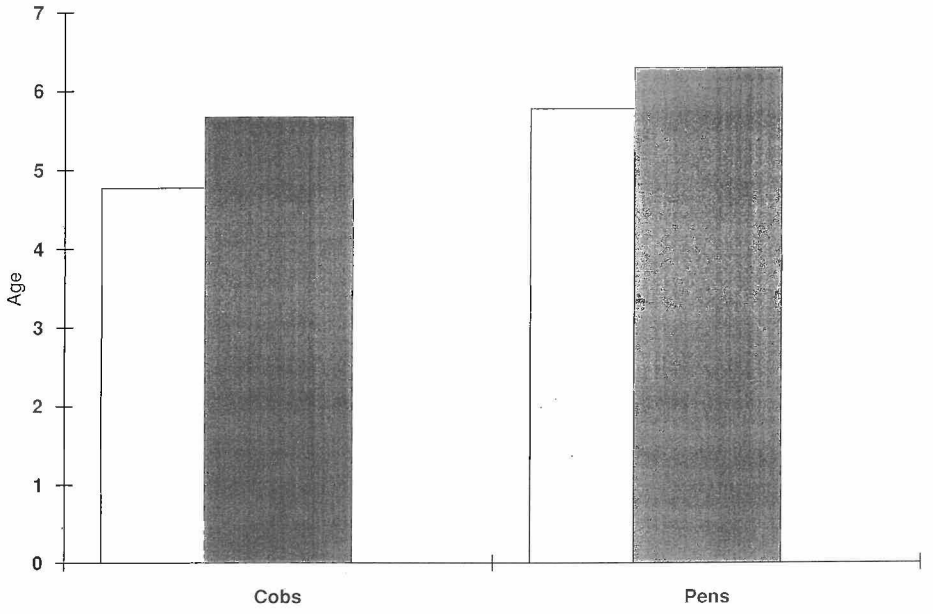

Figure 10. Mean age of parent Mute Swans at nests where a) no young were hatched (open columns) and b) where at least one cygnet hatched (filled columns). The differences are not significant.

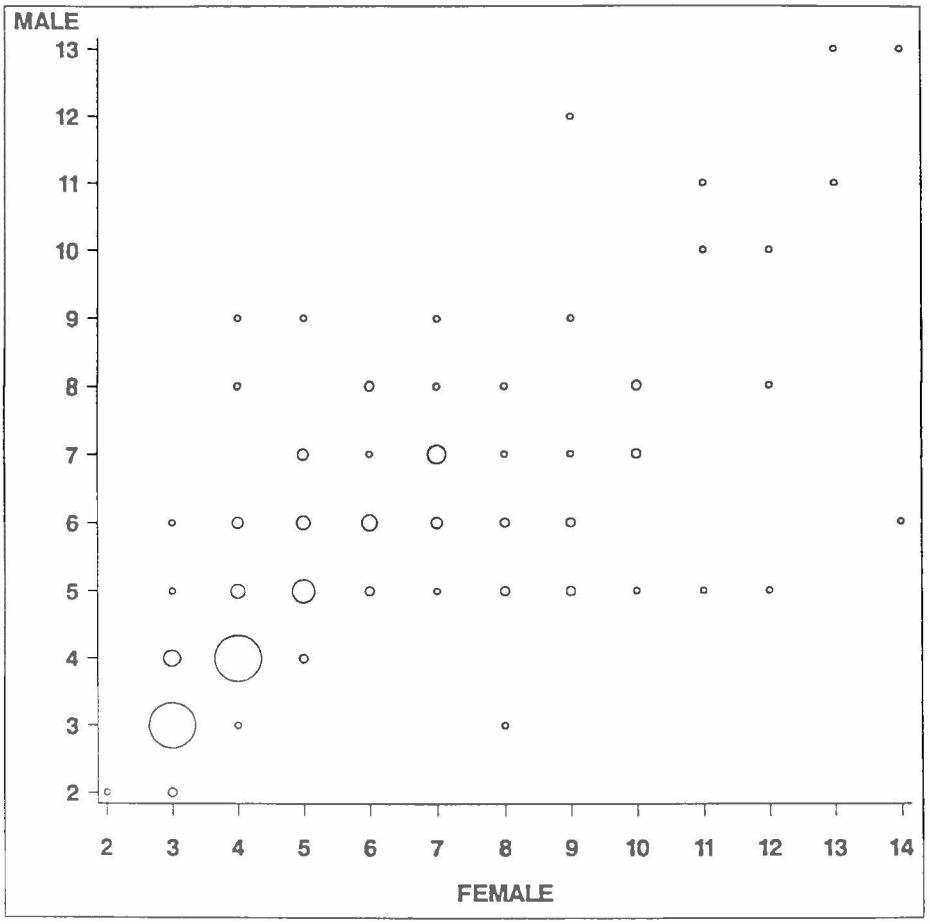

Figure 11. The correlation between the ages of the two members of a pair of Mute Swans: the figure plots only the ages of each pair in the year when they first paired together (see text for further explanation). The Spearman rank correlation is highly significant (0.877, T = 26.21, with 206 degrees of freedom, P = <0.001)

tion between the ages of the two members of a pair would not come about just because young birds, mating for the first time, paired together and then stayed mated together for the rest of their lives. With a mortality-rate as high as that of the Abbotsbury Swans, many birds are soon without their original partner. **Figure 12** shows the data for the numbers of mates that birds have had in relation to the number of breeding attempts that they have made. Of the 14 birds which have bred on 11 or more occasions, four have retained the same mate the whole time. Similarly, for the birds which have bred eight to ten times, well over half of them have changed mates at least once. Hence, many new pairings occur within the colony each year and, although we do not understand the mechanism by which it comes about, widowed old birds show a strong tendency to re-mate with another old bird.

Age Structure of the Population

Figure 13 shows the age structure of the breeding population in 1993. This figure shows the sort of pattern that one would expect from the information on the age of first breeding (**Figure 3**). There were no birds breeding at the age of two, which is not surprising since such birds are rare, and there were progressively more birds breeding from each of the older cohorts until the age of six; after this age, the num-

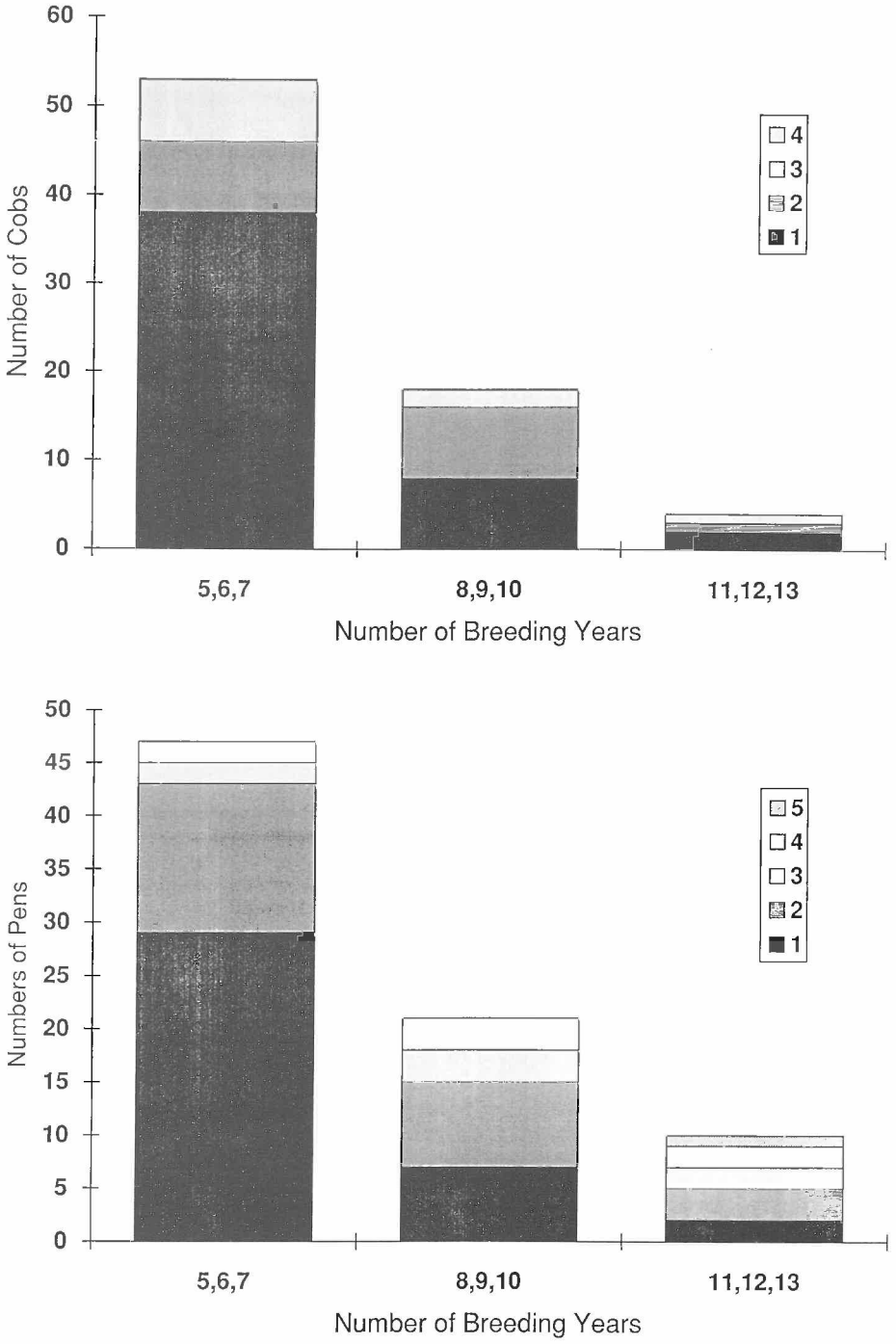

Figure 12. The number of birds to which a Mute Swan has been mated in relation to the number of years for which the bird has been breeding: 12a males and 12b females.

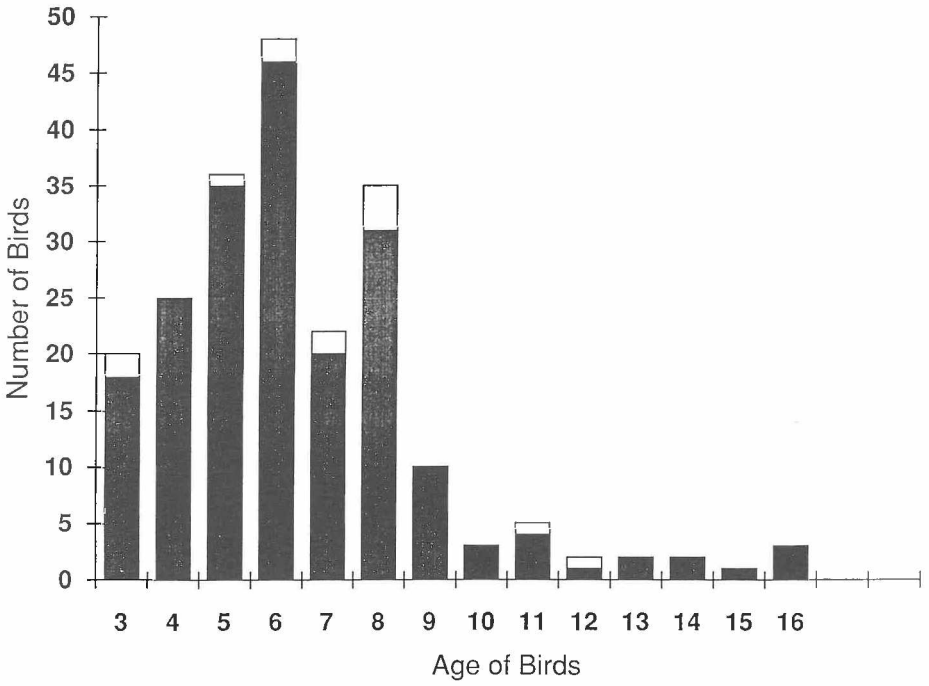

Figure 13. The age distribution of Mute Swans breeding at Abbotsbury in 1993. Solid bars = birds of known age, open bars = minimum age of birds of unknown age (all such birds were assumed to be three years old when they first bred in the colony).

ber dying exceeds the relatively small number of birds which breed for the first time and so the numbers breeding from each cohort declines. The figure also shows the effects of the very bad year for survival 1986-87; this clearly had at least as marked an effect on the 1986 cohort as it did on the breeders. So, there were fewer birds from this cohort breeding (at age seven) than of the older 1985 cohort, even though the latter had suffered one year more of mortality (approximately the same number of cygnets were raised in both these years).

The other point to note is that although the birds aged ten years old or more are the most successful breeders in the population (**Figures 8 & 9**), they form only a very small component of the total population. Out of a total of 228 birds which attempted to breed in 1993, only 18 (7.9%) were aged ten or more. The large majority of the cygnets is raised by the younger cohorts, predominantly by birds which are five to eight years old.

Discussion

There are two puzzles about the composition of the breeding birds. As shown, in recent years, the large majority of the breeding birds were themselves raised in the colony. However, earlier, there were larger numbers of immigrants. There are still large numbers of immigrants which come onto the Fleet either for the winter or to moult. Yet, as the number of locally-born birds has increased, the numbers of immigrants entering the breeding population has decreased. The explanation for this is not clear. There does not seem to be any reason to suppose that there is an upper limit to the 'space' available at Abbotsbury for breeding; the area in the immediate surroundings of the colony is similar to that where the colony is nesting. Hence there is no reason to suppose that birds which really 'want' to breed at Abbotsbury are prevented from doing so. It has been suggested that some of the pairs nesting on the perimeter of the colony seem more aggressive than those in the centre and, if this is the case, it may be more difficult for birds

to add themselves to the edge of the colony. Nevertheless, the colony has increased in numbers in recent years so that it seems as if the structure of the colony is not sufficient to prevent extra birds fitting in.

Also, it should be noted that, in many of the years, the numbers of breeding pairs were well below the maximum number ever achieved (the highest number ever being 130), so in these years there clearly was potential for more breeders had there been other birds which *wanted* to breed in the colony. One possible explanation for the reduction in the number of non-Abbotsbury born birds in the breeding population could be related to their territorial behaviour. The high density nesting at Abbotsbury is unique in the British population; most British Mute Swans are highly territorial and vigorously defend their large territory against intruding neighbours. All non-Abbotsbury born birds arriving at Abbotsbury will have been raised under such conditions. Hence Abbotsbury-born birds may be more 'prepared' to 'accept' the high density conditions at Abbotsbury and so, as the numbers of Abbotsbury-born cygnets have risen in recent years (see above), the non-Abbotsbury-born birds have found the colony progressively less desirable as a nesting site.

A second problem is that colonial-nesting in Mute Swans, including those at Abbotsbury, has been shown to be associated with a genetic characteristic (Bacon & Andersen-Harild 1987). In view of the fact that, especially in the earlier years of this study, such a high proportion of the breeders were immigrants which, presumably lacked this trait, how could the trait be maintained in the Abbotsbury colony? There is little difficulty understanding how this came about in the current situation with low immigration, because the pairs with the 'colony' gene (Aa) raise many more young than those without (Bacon & Andersen-Harild 1987), but with high immigration in low populations, such as those found at the beginning of our study, rough calculations suggest that the maintenance of the colony gene would have only just been possible (Bacon pers. comm.).

The survival of the adult birds is also clearly different from that reported elsewhere in Britain (Bacon & Perrins 1991). Perrins & Ogilvie (1981) showed that this was high, but a longer run of years shows that, while it may be very high, it can also be very low in some years. The Abbotsbury breeders mostly seem to remain on the Fleet the whole year round. They are therefore safe from a number of the main causes of mortality in British Mute swans (Brown et al. 1992), including deaths from lead poisoning (Sears 1989), injuries from fishing tackle (Birkhead 1982) and from flying into overhead wires (Perrins & Sears 1991). It is therefore not unreasonable to expect that they would have a good survival rate. We do not fully understand why this is not so, but there are no really old birds in the colony (by 1993, none of the birds which were breeding in 1976 were still alive).

However, they rely on a natural food supply, primarily of Zostera. This is also eaten by many other wildfowl, particularly Coot *Fulica atra* and Wigeon *Anas penelope* both of which have occurred on the Fleet in considerable numbers throughout this study and Brent Geese *Branta bernicla* which have increased rapidly in numbers in recent years. In addition, there may be up to 400 or so immigrant Mute Swans feeding on the Fleet in winter. Further, the Zostera dies down in the later part of the winter and, in certain years with strong gales from the south, much of this food supply is up-rooted by wave action and thrown ashore. Hence, although some grain is provided, there may be periods of food shortage in winter. At these times, dead birds seem very light in weight and so starvation is a likely cause of death. Nonetheless, no significant die-offs have been reported, nor have numbers of the Abbotsbury Mute Swans been reported as moving elsewhere (the nearest other water is Radipole Lake, Weymouth, where a sudden incursion of Abbotsbury-ringed swans would be noticed). It therefore remains slightly surprising that such a high percentage of the breeding element of the swan population dies in some winters.

The kind co-operation of a number of people has made this study possible. We are grateful to the Ilchester Estate, especially Mrs Charlotte Morrison, for permission to study the birds there. The Swannery staff, especially the Warden, John Fair. Dick Dally, Steve Groves, Don Moxom, David Wheeler and Mrs Ilona Coombs have undertaken much of the recording. A great many

other people have also helped, especially with the roundups and in particular A. E. Coleman and his team. Carl Mitchell has provided much support, especially with the provision of rings. Dr Philip Bacon kindly commented on an earlier draft of the paper and provided much help with the database.

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