Pairing behaviour in a colony of Mute Swans *Cygnus olor*

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A study was made of the Mute Swans present in the breeding colony at Abbotsbury each summer. A large number of the birds do not breed. Some of these non-breeders are probably not yet old enough to breed, but others are birds which have bred in earlier years. In years of low nesting numbers, the numbers of birds which have bred, but are not breeding, may exceed the numbers of breeders. When swans take a new mate, due to death or divorce from the previous mate, they tend to choose a mate closer to their own age than would be expected by chance.

Keywords: Divorce, Age, Mute Swans.

The Mute Swans *Cygnus olor* which inhabit the Fleet in Dorset, breed in a colony at Abbotsbury, at the western end of the Fleet. This colony is unique in the United Kingdom, though colonies exist elsewhere in Europe (refs in Wieloch 1991), particularly in Denmark (Bloch 1971; Anderson-Harrild 1981; Bacon & Anderson-Harrild 1987; 1989) and in Poland (Sokolowski 1960). The colony may be considered to be well-established since there are records of it dating back to 1393 (Birkhead & Perrins 1986).

A study has been made of the birds living and breeding in this colony, starting intensively in 1977. Since then, the number of breeding pairs in the colony has fluctuated between 18 and 130 pairs, though in the last ten years, the number of pairs has not fallen below 50. Even at the start of the study, it was possible to distinguish the birds which had been raised at Abbotsbury from those raised elsewhere because the cygnets raised in the colony at Abbotsbury are marked with a small nick in the web. In an earlier study (Perrins *et al.* 1994), we showed that only a small proportion, some 10% of the females and 20% of the males, of the birds breeding in the colony are immigrants, having been raised elsewhere. We could not, however, determine the age of the breeders at that time, but as the years have gone by, progressively more of the birds have been hatched during the study period and so we do know their age. We have now followed the colony for a full "generation" since none of the birds breeding in 1977 survived to 1995; hence all the birds reared in the colony that are now reproducing there are of known age.

We also showed (Perrins *et al.* **Figure 11**) that there was a strong tendency for the two members of a pair to be of similar age. In part, this correlation probably came about because many new pairs were formed by the pairing together of two young birds who then grew older, gracefully, together. However, this did not seem to be the full explanation because a similar correlation was observed between the two partners in older pairs despite the fact that fewer than half of the birds aged eight years or more were breeding with their first mate (some 60% of males and some 77% of females, who will reproduce

at some stage during their lives, have started to breed by the age of four). Hence the continued correlation between the ages of the two members of a pair appeared to stem from the fact that older birds, when selecting a new mate, tend to choose an older rather than a younger partner.

Although this seemed to be the likely explanation, such selection of a partner is not straightforward. Disregarding the fact that we do not know how the two members of a new pair select one another, we presume that not all birds within the colony are equally "available" as potential mates. The main reason for this is that pairs, both of whom have survived to the following year, tend to remain mated to one another and are, therefore, unlikely to form a new bond. Although there are a small number of divorces, the main sources of potential partners for new pairings are likely to be birds that i) had not bred in the previous year or ii) ones whose mate had died since the previous summer.

The aim of this paper is to examine the mating pattern in more detail and, in particular, to compare the age of birds apparently "available" as partners, with that of the partners selected.

Methods

All birds were ringed with a standard BTO metal ring and with a large, engraved plastic (darvic) ring which enabled them to be identified individually in the field without having to catch them.

We know the exact age of most of the birds associated with the colony since individuals present were themselves raised there in earlier years and were ringed as cygnets. The ages of some of the immigrants are known because they were ringed in their first year (when they can be recognised as one-year-olds by their plumage). The age of other immigrants is not known precisely and pairings that include a bird of unknown age have been excluded from most of the analyses presented in this paper.

There are some problems with the sexes of the birds. Most birds have been sexed by cloacal examination at the time of ringing. The sex of all birds that breed is known and we believe this to be almost always correct; on those (few) occasions where the sex at breeding contradicts that at ringing, we have favoured the former. However, the sex of those birds which are sexed when ringed and for which we have no confirmation of sex at breeding may be less accurate than that for the breeding birds. A further problem is that some 25% of the birds were not sexed at ringing. Since these make up a significant proportion of the pool of birds which are available as potential mates, we could not ignore them in the analyses of the numbers of mates that are potentially available. The sex ratio of the sexed birds is very close to unity (there is a slight trend for there to be more males amongst those birds less than seven years old and for there to be more females amongst those aged eight or more; a trend in keeping with the very slightly higher survival rate of females reported earlier (Perrins *et al.* 1994)). So, we took all the available, but unsexed, birds in each year, divided the number in each age class into two and added one half to the relevant male totals and the other half to the relevant female totals.

We have sporadic sight records of the birds present in the colony at different times of year. These are augmented by bi-annual round-ups (in 1980, 1982, 1984, 1987, 1989, 1991, 1993 and 1995) when the large majority of birds are caught and identified. As a result, we know not only who bred, but also who else was present in the colony, but did not breed, with reasonable, though not perfect, accuracy. For the breeders we identify all those which raise a brood successfully, but in a few cases where the nest was lost early, we may not have the identities of both (or either) parent; so a small proportion of the birds that attempt to breed every year are not identified and this will lead to a small error in some of the results presented. Similarly, a small number of birds may be present as non-breeders during the summer, but are not recorded then. Overall however, almost all of birds present are recorded at some stage during the year. As a result, we can, with reasonable accuracy, examine the age and sex structure of the population in the

summer and, for those breeding birds which have taken a new mate for the season examine the "pool" of possible mates from which the new mates were drawn. We have defined a bird as being available for pairing in any year if it was recorded on the Fleet during the months of March to August inclusive and was more than two years old.

In our analysis of age of mate in relation to that of the birds available as mates, we took all those birds (of the correct sex) which we believed to be present in the breeding season as being potentially available. However, for some of the analyses, especially those involving age, we have assumed that only those birds actually participating in a first time pairing were available as mates. The results of this assumption will usually be conservative since, when we compare this age distribution of birds in new pairings with all those available, we find more two- and three-year olds in the latter group. Thus, if the hypothesis is that older birds tend to choose older mates, this effect would be rendered more extreme by including the younger age classes.

Results

A large number of birds do not participate in the breeding attempts each summer, in spite of the fact that many of them seem old enough to breed or have actually bred in a previous year. In the following sections we examine the non-breeders, the pairing pattern of the breeders and the age distribution of the potential mates and compare the latter with the age of the actual mate which each target individual acquires.

The numbers of birds which are non-breeders in any year

Table 1 shows the actual numbers of each age class which were alive each breeding season, which has bred at least once but which were not recorded breeding in that year. **Table 2** shows, for each year, the status of the birds which had bred at least once. These are divided into birds which i) were breeding ii) had bred, but were neither breeding in the year in question, nor bred in a subsequent year and iii) had bred, were not breeding in the year in question, but bred again in a subsequent year. The last two categories may not be intrinsically different; it may just be that the chances of breeding in a subsequent year are merely a reflection of how long the individuals survive.

Table 1. The number of non-breeding Mute Swans in each year, by age. The large number of unknowns at the beginning of the study relates to the fact that most of these birds were unmarked at the start and so could not be aged.

	3-4 yrs	5-6 yrs	7-9yrs	≥10yrs	Unknown
1981	5	9	4	6	37
1982	3	18	8	5	40
1983	3	14	14	1	16
1984		3	15	3	15
1985		4	10	3	9
1986		1	10	2	9
1987	2	5	23	14	11
1988		1	14	14	3
1989	2	15	9	26	13
1990	1	7	5	16	7
1991	1	4	10	15	8
1992	11	14	27	11	7
1993	2	17	32	20	8
1994	2	21	23	13	1
1995	4	16	41	39	5

Birds which, having bred, skip one or more years

As shown in **Table 2**, a considerable number of birds which have attempted to breed in at least one year did not breed in one or more subsequent season(s) although they were known to be alive. We do not know why these birds do not breed, but some of them miss not one, but several years and yet do breed again (**Table 3**).

We do not know why birds should skip years in this way. The only correlation that we can find is that more birds skip breeding in years when the breeding numbers are low (**Figure 1**). From this figure, it appears that the number of birds which skip a season is low in years when there are more than about 80 pairs breeding, but rises sharply when the breeding numbers fall below this level. In both these figures there is a suggestion of a curvilinear relationship, but the fit of the quadratic regression is only very slightly higher than that of the linear regression.

Table 2. The status in each year of Mute Swans which had bred at least once in previous years.

Year	Breeders No. of pairs	Non-breeders Which never bred again		Non-breeders Which bred again		As % of all birds that have bred	
		Male	Female	Male	Female	Male	Female
77	50	10	6	5	6	23.1	19.4
78	77	12	8	5	6	18.1	15.4
79	83	16	9	11	9	24.5	17.8
80	104	22	15	8	7	22.4	17.5
81	79	47	42	9	6	41.5	37.8
82	52	47	46	11	12	52.7	52.7
83	41	31	28	12	17	51.2	53.3
84	60	26	19	7	11	35.5	33.3
85	80	21	14	2	4	22.3	18.4
86	83	22	15	3	1	23.1	16.2
87	59	43	32	10	6	47.3	39.2
88	85	31	26	2	2	28	24.8
89	68	34	35	12	8	40.4	38.7
90	97	21	21	6	5	21.8	21.1
91	130	24	26	3	1	17.2	17.2
92	108	31	38	9	9	27	30.3
93	114	38	43	5	7	27.4	30.5
94	112	38	43	1	1	25.8	28.2
95	76	56	61	0	0	42.4	44.5

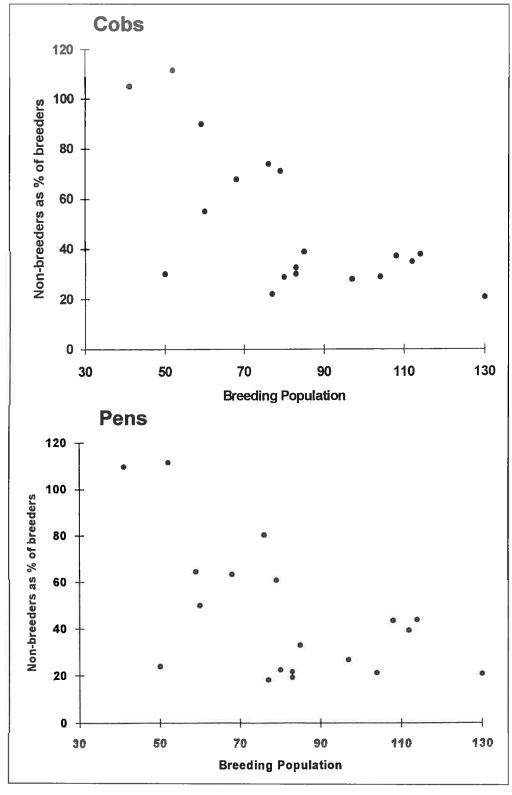

Figure 1. The proportion of Mute Swans which bred in a previous year, but which were not recorded as breeding in the current year as a percentage of the current year's breeding population. Upper figure males (r^2 = 39.7%,P = 0.002), lower figure females (r^2 = 23.0%,P = 0.022).

Table 3. The number of years for which Mute Swans skipped breeding (a bird might skip breeding once for one year and again, later, for two years; if it did this would score as 1 and 2, not as a 3).

Years skipped	Males	Females
n		
1	63	71
2	20	19
3	5	7
4	2	3
5	2	3

Table 4. The number of Mute Swans starting to breed again in a particular year and the number of years that they had skipped.

Year	1	2	3	4	>5	Total
77	6	1				7
78	3		3	1	2	9
79	3	1				4
80	9				1	10
81	4	2	4			10
82	7	1				8
83	7	2		1	2	12
84	11	6	1	1	1	19
85	7	7	1	1	16	16
86	2				2	2
87	2	2			2	2
88	12	2			14	14
89						
90	12	4	2		18	18
91	7	2		1	1	10
92	4				4	4
93	14				14	14
94	7	4			11	11
95	2	1				3

Table 5. The number of male and female Mute Swans which remained faithful to their previous partner in each year. The reason why the numbers are not identical is that a very small number of birds which skipped a year of breeding are counted as faithful to their previous mate if they paired with it again, but if a bird was mated to a different partner and then re-paired with the original one it was obviously not counted as faithful.

Year	Nests	Males	Females
	n	n	n
77	50	4	4
78	77	15	15
79	83	27	27
80	104	47	47
81	79	42	42
82	52	20	20
83	41	14	15
84	60	19	18
85	80	28	28
86	83	38	37
87	59	39	38
88	85	45	44
89	68	50	50
90	97	55	55
91	130	82	81
92	108	81	80
93	114	70	69
94	112	80	80
95	76	53	52

Table 6. Number of years which a pair of Mute Swans bred together, excluding birds that were paired together for only one year. The Table is biased towards shorter pairings because many of the pairs have not yet completed their lifetimes together. In a few cases (33 males, 27 females) the time span over which a pair bred together is longer than that shown, because there are a few cases where birds skipped breeding. All these are for three years or less except for one pair of birds which only bred in three out of nine years.

Years *n*	Males	Females
2	71	66
3	71	63
4	44	39
5	32	28
6	20	22
7	15	16
8	9	8
9	4	7
10	3	2
11		1
12		1
13	1	2
14	1	

Hence the total number of past and present breeders in the colony each summer is rather more stable than the actual breeding numbers. Plainly this is not a density-dependent situation. Since the nesting area available to the colony is more or less constant from year to year, the birds cannot be prevented from breeding because of shortage of nesting sites. This suggests to us that there may be years in which the winter conditions are such that the birds come into the colony in spring in too poor a condition to be able to breed. There might however, be other explanations. For example, in a few years, there have been problems with a Fox *Vulpes vulpes* in the colony whose presence has led to some desertions. While we do not believe that this disturbance has led to many birds not even attempting to breed, it may have discouraged a few pairs from making breeding attempts.

Those birds which have skipped one or more years of breeding show some signs of starting to breed again in the same year. **Table 4** shows that the years in which some birds start to breed again is very non-random, with many two and three year "skippers" starting to breed again in the same year that those who have just skipped one year do so. This again seems to suggest that these birds may rejoin the breeding community when conditions become more favourable.

Mate Retention and Divorces

Many swans remain paired with each other over a series of years and sometimes for many years (**Tables 5 and 6**). From these it can be seen that a high proportion of the breeding pairs each year are comprised of birds that have been paired together for several or many years (as explained above, the pair is not identified at a small number of nests where the eggs are lost early, so that the true number of pairs staying together is probably slightly larger than that shown). Nevertheless, pairs do split up on occasions. We have here defined divorce as occurring when both the birds from a pairing in a year were known to be alive during the following breeding season.

Table 7 shows, for a bird which changes its mate between seasons, the fate of the first mate in the second season. A very small number of birds which divorced and bred with another bird, then re-paired with the original partner again.

One of the reasons why a bird skips a breeding year may be that it only loses its mate (either through death or divorce) just prior to the breeding season and so does not have time to find another one. Minton (1968) also showed that some birds which lost or separated from their partner took more than one year to find another partner and breed again.

Table 7. The status of the two members of a pair of Mute Swans after a breeding attempt in one year was followed by a different pairing the next year. Rows i-iv are subdivisions of the fates of old mates whose partner had taken a new mate.

	Male	Female
Paired with new mate	60	106
i) old mate dead	29	56
ii) old mate breeding with new partner	9	10
iii) old mate not breeding, but bred in a later year	0	9
iv) old mate not breeding and never bred again	22	31

Number of partners in a life-time

Because there is considerable mortality between breeding seasons in most years some birds are widowed each year. At least some of these take new partners and some may have several partners during their lifetime. **Table 8** shows the numbers of partners birds had during their lifetime. It should be noted that this table includes the current breeders and, since these birds have not yet lived out their breeding lives, there will be a slight bias against the larger numbers of partners.

Table 8. The numbers of partners which individual Mute Swan breeders had during their life-time.

	Sex of Bird	
Mates n	Male	Female
1	340	287
2	56	56
3	12	14
4	1	8
5	–	3

Age of mate

There is a high correlation between the ages of birds breeding together for the first time, as can be seen from **Table 9**. We adopt the conservative Spearman rank correlation approach to avoid problems with the somewhat right skewed distribution of ages of birds pairing together for the first time, but the correlation is significant in every year for which we have data. Note that this result is more conservative than our previous result on correlations between ages, since each consortship appears only once in the analysis.

Table 9. Spearman rank correlations between male and female age for Mute Swan pairs breeding together for the first time for the years 1984-1995; 1987 had insufficient information. In all cases except 1992 (when there are only 11 new pairs) the rank correlation is highly significant ($P<.01$).

Year	New pairs *n*	rho	*P*
84	10	0.78	<.01
85	13	0.68	<.01
86	27	0.57	<.01
87	7	–	–
88	29	0.95	<.01
89	16	0.89	<.01
90	28	0.89	<.01
91	35	0.86	<0.1
92	11	0.65	<.05
93	28	0.94	<.01
94	23	0.85	<.01
95	13	0.91	<.01

We compared the ages of two members of a new pair with the ages of the birds apparently available. Each pairing is only counted once, in the first year that it occurred, in order to avoid inflating the sample sizes by including repeat pairings of the same pair. However, an individual bird may score more than once in such a table if it has more than one mate during its lifetime.

A striking feature of the new pairs is the frequency with which pairs of exactly equal age are found. We examined this by calculating the expected frequency of equal age matings on the hypothesis that the birds actually starting a new pairing in any year might have mated at random with respect to age. In many years there are insufficient data for a formal test, but **Table 10** shows that where it is reasonable to test whether equal age pairs are more frequent than expected there is a very strong tendency for it to be so (chi-squared (4) = 119.54, $p<<0.001$). This is further illustrated in **Figure 2**.

Table 10. There is an excess of pairs of Mute Swans with mate of exactly the same age compared with that expected on the hypothesis of random mating amongst the birds forming new pairs in that year. The expected number is calculated as follows. In any year the expected proportion of pairs where the male and female are the same age is p(mage = x)*p(fage = x) summed over ages x = 2 to x = 14, where mage and fage are the male and female ages in whole years. Thus:

$$\text{P(same age)} = \sum_{x=2}^{x=14} \frac{\text{n(m.age = x)}}{\text{n(males)}} \times \frac{\text{n(f.age = x)}}{\text{n(females)}}$$

and the expected number of same age pairs is P(same age) **n*(pairs) we have:

$$\text{Expected No.} = \sum_{x=2}^{x=14} \frac{\text{n(m.age = x) x n(f.age = x)}}{\text{n(pairs)}}$$

In testing the hypothesis that same age pairs are more common than expected, we note that in only five years are the expected values more than five. It is not clear in this case that the expedient of pooling cells to satisfy the requirement that less than 5% of the expected five are less than five would give a correct view of the probability of a same age pair occurring by chance, so we simply calculate chi-squared for the five years, noting that in all the others the actual number of same age pairs is also much more than the expected. Thus we have chi-squared (4d.f) = 119.54($P<<0.001$).

Year	New pairs *n*	Same age *n*	Expected	X^2
84	10	7	2.40	8.81
85	13	6	2.9	3.24
86	27	7	3.3	4.16
87	7	5	2.6	2.29
88	29	22	6.8	34.37
89	16	11	5.3	6.30
90	28	17	5.5	24.35
91	35	23	8.8	22.91
92	11	6	2.6	4.29
93	28	20	6.1	31.60
94	23	14	4.1	24.04
95	13	9	3.2	10.30

We calculated the median age of the birds available as mates in each year and compared this with the actual age of the mate taken. The median age of the available birds was not constant so in our main analyses we retained year as a variable. In **Figure 2** we plot, for each new pairing, the difference between the age of a bird and the age of its new mate against the difference between the age of the bird and the median age of the birds available as mates. Two lines are shown. The null hypothesis is that birds randomly select their mate from the age distribution of the birds available. If this were the case, one would expect to find a 45° slope as shown by the straight line in the figures (for example, if the median age of the birds available was five, a three year old bird pairing with a five year old would score 3-5 = -2, while a ten year old would score 10-5 = 5). Alternatively, if the birds always chose a mate of exactly the same age as themselves, all the points would fall on a horizontal line through zero.

The curved lines in **Figure 2** are the quadratic regression lines through the points, fitted without a constant term (i.e. through the origin). The coefficients are given in **Table 11**. These show that the actual mates chosen fall much closer to the horizontal line than the slope, in other words there is a very strong tendency for the birds to be choosing a mate closer to their own age than to the median age of those that are available. Both regression lines are strongly significantly different from the 45° line, but there are differences between the lines for the two sexes. In the case of the males, the linear slope is not significantly different from zero, though the quadratic term is significant, showing that there is a slight tendency for the age of the female to be slightly greater than that of the male in the very old age classes. For the females, the fit is significantly different from the horizontal. The main reason for this is that the quadratic term is significant (negatively), showing a marked downwards departure from the horizontal as the birds get older. We believe that the difference between the two sexes can be explained by the fact that female survival is slightly higher than that of the males and so there are fewer males than females in the older age classes, leading to an old male finding it easier to find an old mate than the reverse.

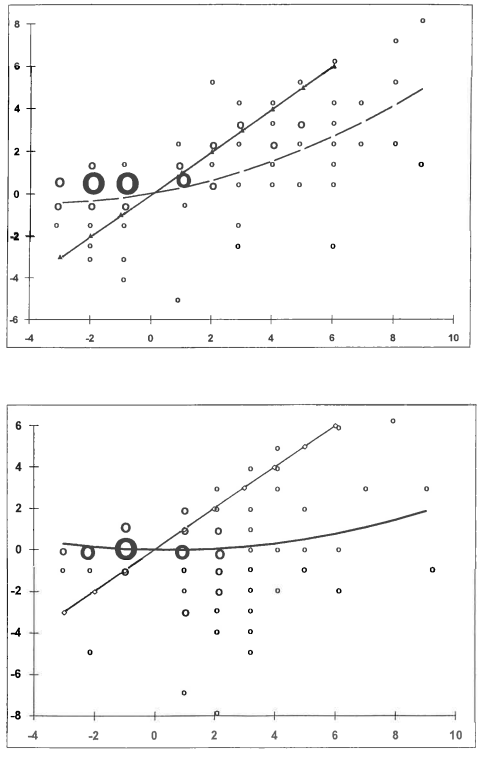

Figure 2. The relationship between the age of the partner and the median age of the birds potentially available as partners of Mute Swans at Abbotsbury; new pairings only. The x axis is the age of the individual – the median age of the birds available, the y axis is the age of the individual – the age of the actual mate. Upper figure is for females, lower for males. The 45° slope shows the relationship if birds always chose mates of median age. The size of the points attempts to show the numbers at that point in the Figure, the smallest points denote 1-2 records, the next 3-5,6-10,20-30 and the largest 43 & 56 in females and 58 in males (n for males = 203, for females = 218). See text for further explanation.

Table 11. Coefficients for a model predicting actual age difference between male and female Mute Swans from a) the difference between the male's age and the median female age for the year and b) the difference between the female's age and the median male age for the year. The model is fitted without a constant term, since the hypothesis of interest, that the actual difference might be equal to the difference between a bird and the median age of potential mates, is represented by the line y=x, which passes through the origin. The linear term for males does not differ from zero, confirming a strong tendency for them to choose same age females regardless of the age distribution of the available mates. The significant quadratic term indicates that for the older males there may be a shortage of females who are old enough, though the effect is slight. The linear term for females differs from 0 (mates tend to be the same age) and from 1 (mates chosen from available age distribution), indicating that females do tend to choose mates closer to their own age, but that for older females there is a shortage of males of the required age for equal age pairings.

a)

Parameter	Estimate	s.e.
Male age – median female age	-0.027	0.066
(Male age – median female age)**2	0.026	0.012

b)

Parameter	Estimate	s.e
Female age – median male age	0.247	0.045
(Female age – median maleage)**2	0.034	0.008

Discussion

Non-breeders

Each breeding season, there are some 500 birds in the Abbotsbury colony of which only some 200 (100 pairs) are breeding. Many of these are not breeding because they are young birds. Perhaps more surprising however, are the quite large numbers of birds which are not only of breeding age, but which have actually bred in a previous year and yet are not breeding at any one time (**Table 1**). In different years the number of these birds may vary from about 20% to about 110% of the breeders. Not surprisingly, there is a very strong tendency for the percentage of each sex which is not breeding to vary in parallel. As shown above (**Figure 1**), the proportion of non-breeding birds is strongly inversely related to the number of breeding pairs, being high in years when the breeding population is low. This strongly suggests that there is a "core" population of potential breeders which varies less than the number of breeding pairs; when a high proportion of these do not breed in any year, the numbers of breeding pairs is low.

Birds which skip a year

Amongst the non-breeders are birds which have already been identified as having had a breeding attempt in a previous year. It is not by any means clear why so many birds, having established themselves as breeders, should then fail to breed in a subsequent year. Since, as shown in **Table 4** there seem to be years when a considerable number of the skippers become breeders again, it seems likely that the birds may be in better condition in some years than others. This suggests that the birds which skip may not be in good condition. We have looked at two circumstances which might show whether it was possible that these birds were out of condition. We have taken those breeding seasons which were before or after one of the recent round-ups (i.e. the breeding seasons of 1993 and 1994 around the July round-up in 1993) and examined the weights and state of moult of the skippers compared with the breeders in each of the two breeding seasons. The weights and moult scores of the skippers at the round-up were not significantly different from those of the breeders in either case. It must be noted that the round-ups are some three months after and nine months before the two breeding seasons so this may not be regarded as very strong evidence.

The age of partners

Divorce rates are reported to be low in Mute Swans (Minton 1968). This is not surprising, since in most situations the pairs of swans are well separated. Indeed where they are on gravel pits or lakes, commonly only one pair occurs there and intruders are vigorously chased away. What divorces do occur include mate-swapping at the edges of territories on rivers. Where birds in isolated territories lose a mate their chances of finding a new partner may be slim. Indeed this seems to be their perception also since at least some such birds go back to the local non-breeding flock at this time , presumably in search of a new mate.

The situation at Abbotsbury is quite different from the normal one for Mute Swans since the birds are nesting in close proximity to each other and there are many non-breeders in the colony, many of these walking around amongst the nests. Hence the birds have an easy opportunity to change mate if they so wish. Nonetheless, changing mate as a result of divorce is still a relatively rare event, with most birds remaining with their mate of the previous year when both are still alive. Since, as mentioned, birds which lose their clutch in the early stages may not be recorded, these figures probably slightly underestimate the degree of faithfulness within the colony.

Minton (1968) also reported that there was a tendency, even amongst older birds pairing together for the first time, for the ages of the two birds of a pair to be similar; Minton also noted that, in such cases, the males tended to be slightly older than the females.

These findings raise at least two questions. First, why do the birds tend to mate with a partner of the same age and second how do they achieve this? There is a good reason for selecting an older mate in that older breeders tend to be more successful than the younger ones. Hence natural selection would favour a bird choosing an older partner, though possibly not a very old one since there is some evidence that breeding success diminishes in the very old birds (Perrins, McCleery & Ogilvie 1994). Further, we do not know how much of the increased breeding success of the old pairs is due to the age of the female or that of the male. Since both sexes appear to choose old mates, this may be taken as evidence that the age of both members of the pair contribute to the breeding success. Given that enhanced breeding success might explain why the birds try to choose an older partner, it does not explain how they do it.

Older birds tend to breed slightly earlier than younger ones, so a bird might theoretically choose an old partner on the basis of some evidence of its readiness to breed at the beginning of the season. However, this seems most unlikely since most pairs are formed well before then and anyway the differences in timing of breeding are small with large overlaps. The birds are clearly better able to identify characteristics of potential partners than we are.

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