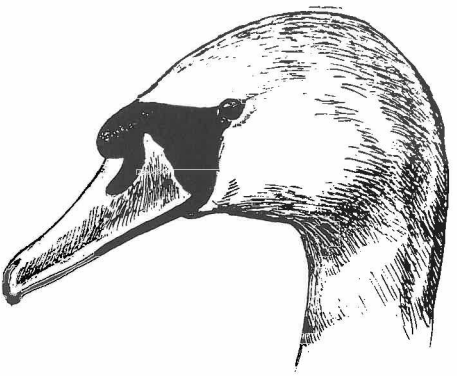
The disadvantage of late-moulting by Mute Swans *Cygnus olor*



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The weights of Mute Swans which have been caught in round-ups on the Fleet at Abbotsbury are examined. Those which have not yet started to moult are lighter than those which are already moulting and survive less well afterwards.

Keywords: Mute Swan, Moult, Weight, Survival

Birds moult their plumage, normally at least once a year. The complete plumage may represent some 20-30% of the total lean dry body mass of a bird (Jenni & Winkler 1994); hence its replacement requires a considerable amount of energy. Calculations of the energetic costs of moult, made by measurements of the energetic value of the feathers, are much lower than those made by measuring the metabolic rates of moulting birds (Murphy & King 1991). The discrepancy arises, at least in part, because moult imposes other metabolic costs on the bird. In addition to the direct replacement of feathers, energy is also required because the birds are less well-insulated and so require extra energy to balance the increased heat loss. There is also increased peripheral blood flow, and an increase in blood volume (Newton 1968) while the feathers are developing. A high proportion of the extra blood is in the developing feather quills which also leads to increased heat loss. Even though the complete moult is often spread over two months or more, the extra energy required, on a daily basis, may be considerable. Moulting passerines may increase their daily metabolism by as much as 13-30% (Lustick 1970, Bancroft & Woolfenden 1982).

Some other features of moult provide suggestive evidence that moult may be costly. For example young birds of most passerine species do not moult their flight feathers when they undergo their first body moult. Within species, late-moulting individuals and those with poorer protein reserves (as measured by pectoral muscle size) may not moult as many greater coverts as early-moulting ones or those with larger pectoral muscles (Gosler 1991, 1994). Dhondt (1981) showed that, for Great Tits *Parus major* moulting in Sweden, late-moulting birds had shorter wings than early-moulters. He speculated that this was a penalty paid for having a second brood (and hence delaying moult) and that it might affect the over-winter survival.

Many of these studies have been carried out on passerines, not wildfowl. In the case of wildfowl, the moult is not studied easily in the wild. Though the birds are flightless at this time they are not caught easily in large numbers. Exceptions to this are some geese and swans, especially the arctic-breeding ones, which can be rounded up. However, even in these cases, the information is usually only based on a single capture of each individual. In some such studies, it has been thought that moult was preceded by an increase in weight so as to enable the (flightless) bird to have reserves for the moult. Some authors have also thought that late-moulting might be disadvantageous, though evidence that this is the case seems sparse. In this paper we examine the fate of Mute Swans *Cygnus olor* which are late in starting to moult.

The study population

Many Mute Swans live on the Fleet, Dorset (c. 50°40'N, 2°35'W). The core of this population is those birds that are raised in, and which live and breed in, the colony at Abbotsbury (Perrins & Ogilvie 1981, Perrins, McCleery & Ogilvie 1994). However, many other birds join the resident birds at various times of year. There are two main periods of the year when many immigrants arrive on the Fleet. One of these is during the last three months of the year. At this time the numbers increase by several hundred, a small proportion of the immigrants are family parties and presumably come for adjacent waters. However, since the winter immigrants cannot be caught easily, little is known about their origins and they depart gradually from December onwards.

There is a second wave of immigration in the summer with as many as 300-400 Mute Swans coming onto the Fleet from May onwards and remaining there for the moult. The majority of these only seem to be on the Fleet during the period from late June until August and they depart again after the moult. The origins of these birds are rather better known because, since the swans are flightless during the moult, they can be rounded up and ringed. All birds are marked with large laminated plastic (Darvic) rings on which a combination of letters or numbers is engraved, making observations of birds possible without recapturing them. The great majority of sightings of these birds, subsequent to their being ringed on the Fleet, come from the Fleet. Those that leave the Fleet tend to go to the west of Abbotsbury, including many parts of Devon and Somerset, but there have been a few sightings of birds as far south as 46°N in western France. For the most part, we have to rely on sightings of these birds by members of the public and such resighting rates are much lower than for those that remain on the Fleet.

The resident population behaves rather differently. They tend to stay on the Fleet the whole year and breed there, and the majority of the breeding population (currently some 80-90% and higher for females than males) is made up of birds that were themselves raised at Abbotsbury (Perrins, McCleery & Ogilvie 1994). Nonetheless, it must be stressed that this distinction is not absolute, the remainder of the breeding population is made up of birds that have immigrated to the breeding colony and a small proportion of the birds which have been raised there leave and breed elsewhere. The proportion of immigrants breeding in the colony has decreased over the years (Perrins, McCleery & Ogilvie 1994). In this paper, the two terms, immigrants and residents, refer to the origins of the birds, not their current status (i.e. some immigrants may remain in the Abbotsbury colony, some Abbotsbury born birds leave it).

This paper examines some aspects of the moult of the birds, particularly those caught in the three round-ups, on 22 July 1989, 20 July 1991 and 24 July 1993 when 706, 614 and 832 respectively were caught and examined.

Methods

At the round-up, the birds are herded into a pen on the land, examined, ringed if necessary, weighed and then released. Though in each catch there was a significant number of unringed birds, the majority of the birds were ringed already and their sexes and ages known. Since all the cygnets at the swannery are ringed each year, it follows that all the unringed birds are immigrants, having been raised elsewhere. Eventually the very large majority of these birds will leave the Fleet again, though a small number remain and eventually enter the breeding colony. In addition, all birds have their state of moult recorded. This is done on the basis of the moult of their flight feathers. The birds are subdivided into six groups: unmoulted, in which the feathers have not yet been shed, and those which have moult scores of one to five which range from where the feathers have just been dropped, but the new feathers have not yet started to grow, through to fully-grown new feathers. At each round-up some birds have escaped, mainly by being able to fly, hence the catch is not complete. Also, amongst those birds caught there are many that should, apparently, be able to fly, either because they have not yet started to moult or because they have

completed it. These birds can be separated on the basis of the state of their primary feathers, which are either clearly worn or quite fresh. Birds which are caught could be a biased section of the population, but this is not thought to be likely to greatly affect the results present here: in 1989 only a very small number of birds avoided capture, in 1991 about 150 birds escaped (mostly by flying), while in 1993 about 80 escaped, some 50 of these being breeders ashore with their broods.

We have large numbers of sightings of many of these birds, so that we can look at their survival subsequent to a round-up.

The statistical tests presented in the tables are all pair-wise comparisons, two-tailed where appropriate. The following convention is used for statistical probability: P=<.05:*, P=<0.01:**, P=<0.001:***, P = <0.0001:****.

Results

Table 1 shows the mean weights of all birds by their moult class at the time of the round-up. In all three years, birds that had not yet started to moult were significantly lighter than those which were already in moult, the difference being quite large, of the order of 0.5 kg. Before jumping to the conclusion that this result represents a difference in condition, we need to be sure that it is not due to differences in the timing of moult between classes of birds whose weights would be expected to differ. Three obvious hypotheses need examining.

First, it is well-known that male Mute Swans are heavier than females and this is clearly supported by the data considered here (**Table 2**). In each year the females were some 1.3 kg lighter than the males. It is not clear whether one would expect this to give rise to our result because in breeding pairs, the

Table 1. The weights (kg) of unmoulted Mute Swans compared with those in which moult had started. The birds are divided by status (Res=resident, Imm=immigrant).

	Moult:	0		1:5		*P*
		n	Weight (kg)	*n*	Weight (kg)	
1989	Res	26	8.11	330	8.77	**
	Imm	37	8.71	232	9.13	**
1991	Res	96	8.61	269	8.95	***
	Imm	28	9.28	143	9.74	ns
1993	Res	89	8.56	450	9.08	**
	Imm	44	9.18	172	9.72	**

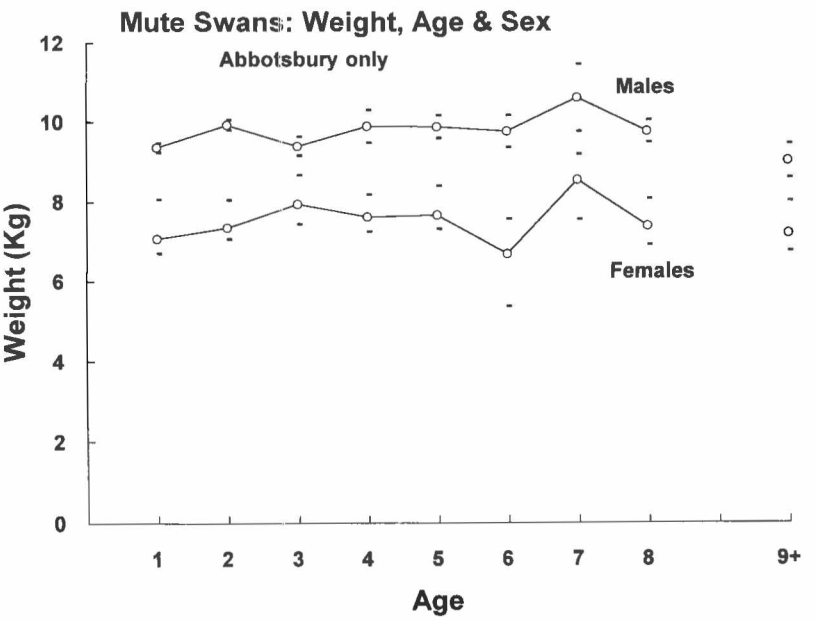

Figure 1. Weight in relation to age for male (n=181) and female (n=185) Abbotsbury born Mute Swans of known age caught at the 1993 round-up. Birds older than eight years are grouped as "9+"; there were 12 males and 23 females. The - marks the standard errors.

female normally moults before her mate so that one would expect the unmoulted group to contain more males and to be heavier, rather than lighter as we found. In fact, the majority of birds are not breeders, being either immatures or failed breeders and, in our sample, the males do not seem consistently to moult after the females (**Table 3**).

A second problem is that the birds' weight and timing of moult might vary with age. There is no evidence that this is so (**Figure 1**), although the stage of moult is affected by age, since a lower proportion of birds aged more than one year have started to moult by the round-ups than is the case with one-year-old birds (**Table 4**). Thirdly, it could be true the immigrants which are heavier (**Table 1**) also moult earlier. However, there is no difference between the proportions of late-moulting birds in the two populations (**Table 5**).

As far as survival is concerned, there is a problem with lumping immigrants with residents (**Table 6**). Because observations are much more intensive on the

Table 2. Mean weight of Mute Swans by sex. Resident birds only.

	Sex	*n*	Weight(kg)	*P*
1989	M	279	9.55	
	F	269	8.23	****
1991	M	201	9.77	
	F	159	8.41	****
1993	M	269	9.85	
	F	252	8.52	****

Table 3. The percentage of Mute Swans which had not started to moult by the round-ups, divided by sex.

	Sex	Unmoulted *n*	Moulted *n*	%	$P(\chi^2)$
1989	M	35	226	13.4	
	F	23	231	9.1	ns
1991	M	52	139	27.3	
	F	41	98	29.5	ns
1993	M	51	188	27.1	
	F	35	197	15.1	ns

Table 4. Percentage of one-year old Mute Swans versus older ones which had not started to moult by the round-ups.

	Age	*n*	% not moulted	$P(\chi^2)$
1989	1	110	4.5	
	>1	277	9.4	ns
1991	1	169	13.1	
	>1	262	32.4	***
1993	1	197	9.5	
	>1	434	24.4	***

Table 5. Weight of Mute Swans in relation to status.

	Status				
	Resident		Immigrant		*P*
	n	Wt(kg)	*n*	Wt(kg)	
1989	378	8.74	283	9.08	***
1991	396	8.87	199	9.65	****
1993	580	9.04	245	9.66	****

Table 6. Percentage of Mute Swans seen again after the round-ups.
Res-resident, Imm=immigrant.

	Status	*n*	Seen again	%	$P(\chi^2)$
1989	Res	387	327	84.5	
	Imm	289	125	43.1	***
1991	Res	409	353	86.3	
	Imm	205	88	43.1	***
1993	Res	584	412	70.5	
	Imm	246	73	29.7	***

Table 7. Mean weight of Mute Swans divided by sex and moult score. Abbotsbury residents only. (*) denotes a Probability of 0.054

	Sex	Moult	*n*	Weight(kg)*P*
1989	M	0	14	8.45	
		1:5	128	9.35	*
	F	0	8	7.29	
		1:5	121	8.18	****
1991	M	0	50	9.36	
		1:5	138	9.87	**
	F	0	124	8.75	
		1:5	412	9.22	***
1993	M	0:1	63	9.28	
		2:5	88	9.78	**
	F	0	25	7.94	
		1:5	132	8.34	(*)

Fleet, the Abbotsbury birds have a much higher chance of being recorded subsequently than do the immigrants. Hence, because their probability of being re-sighted in so much lower, the differences shown in **Table 6** cannot be considered as evidence that the immigrants have a lower chance of survival. Much, perhaps all, of the difference must be attributed to the reduced probability of re-sighting of the immigrants once they have left the Fleet. Because of these findings, immigrants have been excluded from most of the analyses presented here, age has not been taken into account and the samples are divided by sex.

Table 7 shows the weights of birds, divided by sex, in relation to whether or not they had commenced their moult. After removing all the possible confounding factors mentioned above, the weight of birds that had not yet started to moult was significantly lighter than that of those that had commenced

moulting. The difference holds in each sex and in each year and is therefore fairly robust. There were not consistent differences between the groups of birds with other moult scores, although in 1993, those with a moult score of one were no heavier than the unmoulted birds and significantly lighter than the other moulting birds. In 1989 and 1993, birds with moult scores of four and five (i.e. those which were first to start moulting) were significantly lighter than those with a moult score of one to three (**Table 8**) and about the same as those which have not started to moult.

An obvious question to ask is whether late-moulting puts the birds at any disadvantage. The question can be answered by examining whether or not the birds are seen again at a later date. **Table 9** shows the results. Because the birds remain on the Fleet and are recorded intermittently during the year, it did not seem appropriate to use a complex survival model. We have here used the simple criterion of whether or not each bird was recorded alive at any date after each round-up and tested the differences with χ^2.

Pooling data for both sexes, late-moulting birds are significantly less likely to be seen again in two of the three years (and the difference in the third year is almost significant). In this case there seems to be no reason to separate the sexes since we know that their survival is very similar (Perrins, McCleery & Ogilvie 1994).

In **Table 8** where the weight of the earliest moulters is compared with the rest of the birds in moult, there was some evidence that the earliest birds were not so heavy as those moulting later. Using the same divisions of the data, there is no evidence for a difference in survival rate between two groups (**Table 10**). In 1989, the 166 birds which had only just started to moult (moult score one) had a survival similar to that of those that had not yet started to moult and significantly lower than that of those which were more advanced with their moult, but this was not apparent in the other two years.

Discussion

Most wildfowl moult all their flight feathers simultaneously and so become flightless (Owen & Black 1990). In some, a weight loss during the moult has been recorded (e.g Hanson 1962, Owen & Ogilvie 1979) although in others such losses are small (Ankney 1979). It has sometimes been assumed that the birds lay down reserves for the moult before they are flightless in order to help them survive the moult - a time when they may need good supplies of food and when they cannot change feeding sites readily, should they need to. Van Dijk & van Eerden (1991) showed that moulting Mute Swans lost weight at the rate of about 25 g per day. Others have suggested that the weight loss may be beneficial in that the bird's flightless period will be reduced if it is lighter. Certainly Mute Swans fly again before their feathers are fully grown (Mathiasson 1973) and it must be easier for lighter birds to do this.

In this study, birds that had not yet started to moult were lighter in weight than those which had already commenced moult. It is possible that some of these birds were not going to moult at

Table 8. The weight of early-moulting Mute Swans compared with later ones. Abbotsbury residents only.

	Moult	*n*	Weight(kg)	*P*
1989	1:3	497	8.99	
	4:5	85	8.55	***
1991	1:3	359	9.19	
	4:5	53	9.42	ns
1993	1:3	567	9.34	
	4:5	54	9.01	**

Table 9. Survival of Mute swans in relation to moult score. Abbotsbury residents only. (*) denotes a Probability of 0.053

	Moult	*n*	Seen again	%	$P(\chi^2)$
1989	0	22	14	63.6	
	1:5	250	220	88.1	**
1991	0	70	52	74.3	
	1:5	138	122	88.4	**
1993	0:1	56	32	57.1	
	2:5	254	179	70.5	(*)

Table 10. Percentage of moulting Mute Swans seen subsequent to the round-ups, comparing early (4-5) and later (1-3) moulting birds. Abbotsbury residents only.

	Moult	*n*	Seen again	%	$P(\chi^2)$
1989	1:3	500	335	67	
	4:5	85	65	76.5	ns
1991	1:3	364	274	75.3	
	4:5	54	35	64.8	ns
1993	1:3	570	338	59.3	
	4:5	54	36	66.7	ns

all. Little seems to be known about whether Mute Swans ever skip a moult although this is probably very rare if it occurs at all. There is a clear case where a Whooper Swan *C.cygnus* did not moult in one year (Campbell & Ogilvie 1982).

Assuming that they will eventually moult, there seems to be two possible explanations why the late-moulters were lighter: that these were perfectly fit birds, but just ones which were naturally late-moulters, who had not yet put on weight to tide them through the flightless period, or that they had not been able to lay down adequate reserves and were therefore deferring their moult until they could do so. Such an argument holds that the birds were forced to be late-moulters by being in "poor condition" in some way.

The data on subsequent survival of the late-moulters strongly suggest that at least some late-moulters are seriously disadvantaged in some way. Compared with the other birds moulting at Abbotsbury, a higher proportion of the late-moulters are going to die, and the fact that they are lighter than those that have already started to moult suggests that they are not in good condition even in midsummer.

Nevertheless, it also appears that some of these birds are habitually late-moulters. Comparing the three round-ups, we have ten birds which were scored as being unmoulted in both 1989 and 1991, six in both 1989 and 1993 and 20 in both 1991 and 1993 (these figures include three birds which had not started to moult at any of the three round-ups). Presumably therefore, both of the possibilities listed above are true, some birds are habitually late-moulters whereas others are in poor condition and unlikely to survive.

It was also noted that some of the earliest moulters, i.e. those that had started to moult first were not significantly heavier than those that had not yet started (**Table 8**). Since these birds do not show a diminished survival, the most reasonable explanation for this seems to be that they did put on fat for the moult but, as they are nearing completion of the moult, they have nearly used up their reserves. Such a suggestion is in line with the work of van Dijk & van Eerden (1991), cited above, where the Mute Swans lost weight during the moult.

Little seems to be known about the disadvantages of being a late-moulter. In the case of arctic-breeding geese, the birds might be seriously disadvantaged if they were not able to depart in the autumn before bad weather sets in. Mute Swans take some 60-67 days to complete the replacement of their flight feathers, although they can fly a few days before the feathers are fully grown. Hence these late-moulters would not have been airborne again until mid September at the earliest, by which time most of the immigrants had already left the Fleet and the autumn equinoctial gales may have started.

It is clear that late moulting is disadvantageous in the Mute Swan and one can identify the birds which are at risk as early as July when the round-ups take place.

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