Mute Swan weights in relation to breeding

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Introduction

In the course of a general study of the Mute Swan *Cygnus olor* of the Upper Thames valley, a considerable amount of weight data has been obtained. This paper analyses these weights and attempts to relate them to some aspects of the breeding of this species.

Details of some other aspects of this study are given elsewhere (Perrins and Reynolds 1967) and need not be repeated here. The main study area extends radially for about 25 km. from Abingdon (51°40′N., 1°17′W.). It contains about 95 km. of the River Thames together with the lower reaches of several of its tributaries, and many gravel pits and small lakes. The area is largely surrounded by higher ground, up to 200 m., which holds few swans, whereas the approximate mean height of the river valleys (and nests) is 60 m. above sea-level.

Since 1966, the early summer population of swans has dropped from 450-500 to 300-350 (110 to 80 breeding pairs). The non-breeding flocks are now composed mainly of first and second year birds, whereas earlier, up to a third would be three years or older. This decrease has been observed elsewhere (Minton 1971). The main flocks are at Abingdon (40-90 birds) and Oxford (now usually only 30 birds, but up to 100 in the past), and there are several smaller flocks in rural areas. There are also large numbers in Reading, just south of the main study area.

Nearly all the study population have been ringed, and many individually colour-ringed. Considerable numbers have also been ringed at Reading. The majority are of known age when ringed, i.e. in their first or second years. Since 1967, a high proportion of the swans caught have also been weighed, and more recently sexed by cloacal examination. Swans are weighed only when caught for ringing, colour-ringing, the removal of fish-hooks or in a few cases the identification of nesting adults. The mass round-ups, used elsewhere, have not been employed and the swans have remained comparatively tame and easy to study. This policy does, however, result in considerable unevenness in the season and age distribution of swans weighed. Most weights have come from flock birds during the winter. These comprise immatures together with some of the breeding birds. The majority of nesting adults stay on their territories unless the weather is very adverse.

A simple technique is used for weighing swans. Upon capture, two strips of cloth are used to tie the wings and feet together. The hook of the balance is inserted under the strip holding the wings. All the weights have been taken to the nearest 100 gm. The swans are not usually tied in this manner for more than a few minutes. As with all other stages of capture and processing, weighing is usually carried out by one person.

The following analysis is based on 947 weights from 574 swans of known sex (295 females, 279 males) taken in the main study area up to 31st March 1972. In addition the weights of 100 swans at Reading are given for comparison. The majority were sexed cloacally, but many by behaviour while subsequently nesting or occupying territories. The weights of a further 70 birds have been discarded as their sex is as yet unknown. In all the tables, means calculated from less than 10 weights are shown in parentheses.

Weights

Mean values

The means together with the standard deviations and observed ranges, are given in Table I for each age and sex class used. The year has been divided into two periods. 'Winter' comprises the months September to March and, for first and second winter males and first winter females only, April. For these latter categories the April weights are similar to those in winter but differ considerably from the summer ones. This can be readily seen from Figure 1. The third year and older birds have been separated into two groups. The first (adults) are known to have nested or held a territory (and may have nested) in the relevant year. The second (non-breeding) are those which apparently have not bred or whose summer activity is unknown. The summer adult females do not include eight weighed in early April. These had a mean of 10.65 kg. (range 9.7-11.7 kg.), demonstrating the large weight gains made before egg-laying. Similar gains are probably made in March by the early nesters, but none as yet have been weighed.

It can be seen from Table I that the mean weights increase considerably during the first two years. The male weights appear more variable than those of the females. There is a considerable difference between the weights of adults and non-breeding birds of both sexes. There is

Table I. Weights (in kg.) of Mute Swans in the study area.

Age class	Males: Sample size	Males: Mean	Males: S.D.	Males: Observed range	Females: Sample size	Females: Mean	Females: S.D.	Females: Observed range
1st winter	159	9.69	0.73	8.1-12.1	221	7.82	0.79	5.5- 9.5
1st summer	42	10.87	0.98	9.3-13.5	36	8.34	0.72	6.4- 9.7
2nd winter	112	10.43	0.93	8.9-13.0	75	8.42	0.74	6.1- 9.8
2nd summer	16	11.19	1.19	8.9-13.4	12	9.08	0.77	7.9-10.2
3rd winter and older non-breeding	86	10.34	0.91	8.4-12.7	45	8.36	0.69	7.6- 9.7
3rd summer and older non-breeding	8	(11.05)	—	9.7-11.8	4	(8.48)	—	7.7- 9.9
Adult winter	59	11.80	0.89	9.2-14.3	35	9.67	0.64	7.6-10.6
Adult summer	21	11.87	0.83	10.6-13.5	6	(9.65)	—	8.3-10.8

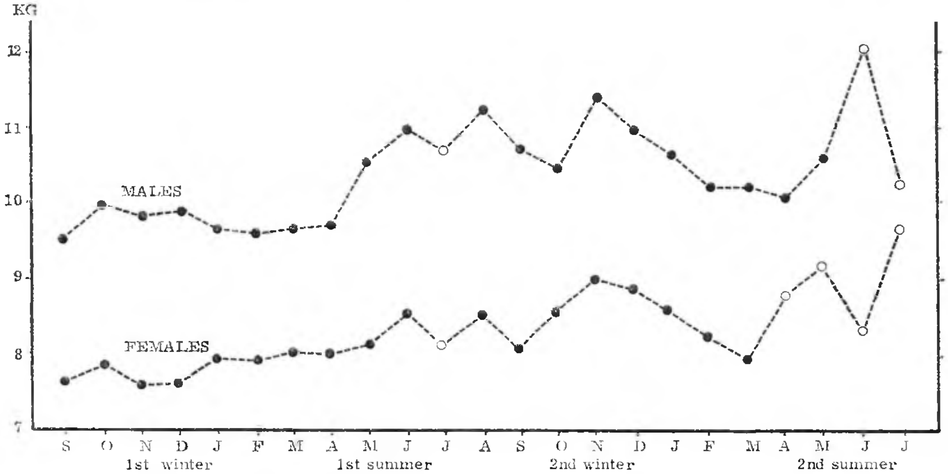

Figure 1. Mean monthly weights in the first two years from fledging. Means for samples of less than 5 weights are indicated by open circles. The standard errors are 0.1-0.2 kg. in the first winter and up to 0.4 kg. later.

little difference between winter and summer for the adults (except for April females), but there is a considerable difference between the two periods for the non-breeding males.

Table II gives the values for the small sample of weights from Reading, only just over 30 km. from Abingdon. Surprisingly enough, the first and second winter males are significantly ($P<0.05$) heavier. There is comparatively little interchange between Reading and the study area. The North Berkshire Downs and Chilterns probably form a natural boundary, with only a narrow gap for the Thames. It has been shown elsewhere (Minton 1971) that Mute Swans prefer to avoid high ground. It is possible that the differences in weights are due to the feeding for cygnets being better on the Kennet, a clean chalk river just south of the Downs, than in the study area. Some cygnets ringed while still on their natal territory in the south of the study area have been weighed in their first winter in Reading, and these were on the light side for the Reading birds, but normal for the study area. The two heaviest swans yet weighed were both first year birds in Reading (14.8 kg. in December, and 15.0 kg. while flightless in June).

Monthly variation

Figure 1 shows the mean monthly weights for the first two years. For most months except in the summer there are samples of at least 5 (14-35 in the first winter). It can be seen that the mean weights of newly fledged cygnets in September is hardly lower than in the rest of the winter. In fact, during the first winter the mean weights are fairly constant, and there is little change until May when they begin to rise just before the moult. Newly flightless first summer birds (199 over six years) have been recorded from 29th May until 12th August, with a mean date of about 5th July, and a standard deviation of about 15 days. There was little difference between the sexes, except that the spread was slightly less for females. There was a tendency for the heavier swans to moult earliest.

In the second year the decline in mean weights of flock birds in the late winter may be partially due to the heavier birds moving out to find territories. This applies especially in recent years, when quite a few second year birds have nested. The absence of a similar decline in the first year birds supports this argument. However, it is possible that the lighter first year birds die off owing to food shortages thus leaving the average unchanged. Yet the lightest female weighed in winter (5.5 kg. in December) survived to at least her second winter. Again, the average weight increase for birds weighed in both their first two winters were 0.66 kg. for females (21 birds) and 0.65 kg. for males (14 birds), very similar to the differences between the population means (0.60 and 0.73 respectively).

The second summer samples are rather small. For birds actually in moult and aged at least two, the average weights were 9.7 kg. for females (3, 9.4-9.9 kg.) and 12.0 kg. for males (6, 11.0-13.4 kg.).

Variations between years

For the first and second winter weights, the samples are large enough to examine the differences between years. However, the second winter means are probably affected by the decreasing population which would allow more younger birds to leave the flocks, hold territories and perhaps breed. This would superimpose a weight decline over the years for this group. Thus it seems only valid to look for annual differences in the mean weights for the first winter samples.

Table III gives the mean weights and sample sizes for the first winter weights for the different years. The last five years have reasonable samples and it can be seen that the means fluctuate in parallel for the two sexes, but with more marked differences in the females. The latter are just significant at the 5% level, but not those for the males which have larger standard deviations. There are thus some indications of weight differences from year to year, perhaps influenced by the summer conditions, or the proportion of early broods. It may be possible in the future, with more data, to investigate whether the first winter weights, and later weights, can be related to the nest site, parents and/or laying date.

Table II. Weights of Mute Swans in Reading.

	Males			*Females*		
Age class	*Sample size*	*Mean*	*Observed range*	*Sample size*	*Mean*	*Observed range*
1st winter	22	10.55	9.1-14.8	18	7.93	6.3- 9.2
1st summer	10	12.22	9.7-15.0	6	(9.77)	8.4-10.3
2nd winter	20	11.48	10.0-14.4	13	8.69	7.2- 9.7

Table III. Mean first winter weights for different years.

		1966	*1967*	*1968*	*1969*	*1970*	*1971*	*All*
Male	Mean	(9.15)	9.71	9.54	9.79	9.61	9.76	9.69
	Sample	2	20	25	51	37	24	159
Female	Mean	(7.90)	7.72	7.57	8.04	7.72	7.78	7.82
	Sample	5	15	36	82	71	12	221

Some relationships between weights and breeding

Late winter weights and summer activity

As the majority of the swans which have been weighed at an age of more than two years have also been colour-ringed, it has been possible to determine the summer activities of a large proportion of those known to be alive. These activities can be divided into 'Nesting', 'Territorial' and 'Non-breeding'. The first category is obvious, but the others need defining. 'Territorial' implies that the swan was paired and held a territory for several days at least, but was not actually proved to have nested. This applies especially to late nesting birds and those who lost their clutches from predation or flooding. The proportion of genuine non-nesting territorial birds is far lower than in Staffordshire (Minton 1968). 'Non-breeding' covers all the birds which are known to have been non-territorial and in the flocks between late March and early May. Some birds were not located during the summer, but were known from later observations to have been alive. This group probably contains territorial and perhaps even a few nesting birds, together with non-breeding birds which moved to other flocks, but for present purposes it is termed 'Unknown'.

Figure 2 relates the weights of swans in January, February or March to their subsequent activity in summer. All these weights are obtained from birds in the flocks when they were more than two years old. In several cases there are two or more weights from the same swan in the same winter. It is clear that normally swans need to attain weights of 10.6 kg. for males and 8.8 kg. for females, before they can hold a territory and breed, in this study area. There have been only one male and two female breeding swans and one territorial female below these limits and one definite non-breeding male above the limit. One male caught in his 5th, 6th and 7th winters weighed 10.1, 10.5 and 12.2 kg. respectively. In the first two following summers he was non-breeding, while in the third he was territorial, but probably did not breed. That spring was late and only one new nesting pair was found instead of the usual 15-20. The 'Unknowns' (16 males and 10 females) were scattered both sides of the limits, as would be expected from the composite nature of this category.

The two males differing from the normal pattern were both weighed in 1967, when the breeding population was high. They were both weighed three times during the winter and their weights have been joined in Figure 2. The light nesting male's mate was found on eggs in late May (i.e. a late or replacement clutch) and he too could have been a 'replacement' for an earlier male who died during the spring. Alternatively, as his weights were showing an increase, it is possible that he passed the normal limit before the pair took up the territory. The heavier non-breeding male was not recorded for a few days in late March. However, his future mate for the following four years was already nesting with her current mate, so it is very probable that he was non-breeding. The single low-weight female may well have put on weight before returning to her nest site. She was a past breeder who had briefly brought her brood into the flock.

Even if it is assumed that all the 'Unknowns' were non-breeding, the separation at the weights is still highly significant ($P<0.1\%$) for both sexes (after continuity corrections, $\chi^2=14.3$ for females and 26.6 for males, compared with 10.82 for the 0.1% level with one degree of freedom). Each individual has only been counted once at its highest weight.

The time of breeding

Before attempting to interpret the adults' weights, it is necessary to know when breeding takes place. The easiest parameter for this is the date of laying of the first egg. Mute Swans in this area appear, without exception, to lay on alternate days, usually during the morning. One egg was observed being laid at 10.15 G.M.T. The newly laid egg appears fresh and clean, but gradually the freshness fades until after two days the eggs are indistinguishable. If the freshest egg can be dated, that of the first egg can be deduced, assuming that no eggs have been taken, and further visits will obtain the full clutch size. If the latter and the date of hatching are known, an estimate of the first egg date can again be made.

The average incubation period appears to be 35 days (based on clutches for which precise information is available (4 of 34 days, 11 of 35, 3 of 36).

Figure 3 shows the relationship between the date of the first egg and clutch size. As can readily be seen the clutch size decreases as the spring progresses. The line of regression (and correlation coefficient) has been calculated for clutch size on date using the 120 definite first clutches. The seven known repeat clutches have not been used for this calculation, but they did not differ significantly. The clutches are mostly from the years 1966-1971, but there are a few for 1952-1965. Taking 1st April as day 0, the regression equation for clutch size (E) on date (d) is $E=7.93-0.098d$. The standard error of the gradient is 0.0075. The correlation coefficient is -0.78 which for this sample size is highly significant. The regression lines calculated for the different years (or year groups for small samples) are nearly parallel and separated by less than a day. The mean clutch size is 7.52, which is higher than earlier figures (Perrins and Reynolds 1967). Only completed clutches have

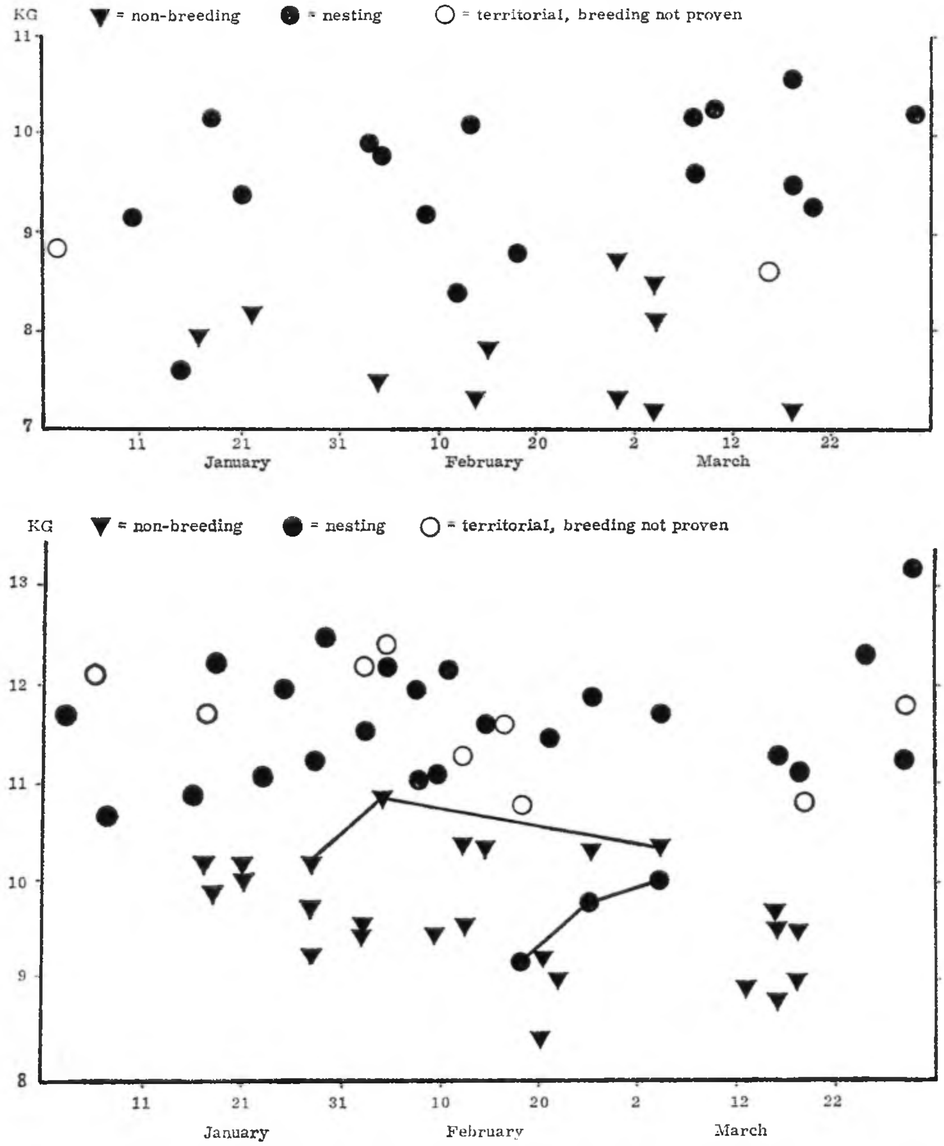

Figure 2. Late winter weights of third year and older Mute Swans in relation to their subsequent summer activity; (above) **females,** (below) **males.**

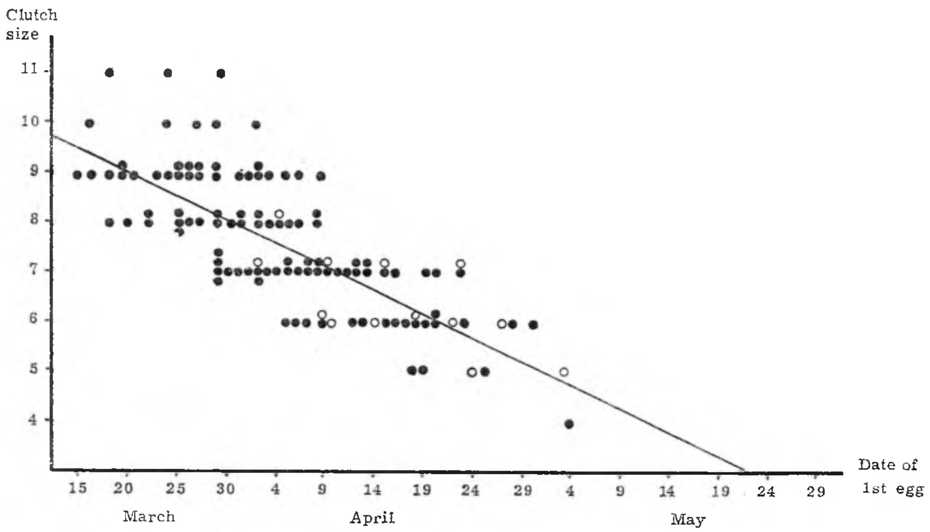

Figure 3. Clutch size in relation to the date of the first egg.

been considered here. There is also a bias towards large clutches. For a clutch of 11 eggs the date of the first egg may be determined on any of the 22 days of the laying period, whereas for a clutch of four it is only possible on eight days. In addition late nests, i.e. smaller clutches, are less likely to be re-visited to determine the full clutch because little time is available outside the school holidays.

Only 13 clutches are from females known to be breeding for the first time and these are shown on Figure 3 by open circles. Another 13 from the earlier years have no record in the previous year either of breeding or non-breeding. The remaining 94 clutches are from females known to have nested in the previous year.

It can be seen that the clutch sizes of first-time breeders tend to be lower than those of past breeders. Age does not otherwise appear to have a significant effect. Individual females may vary considerably from year to year in both clutch size and date.

As there is this strong correlation between large clutch size and early laying (with a gradient of approximately $-1/10$ egg per day for the regression line), there must be some selection pressure acting in favour of early breeding. The early clutches are initiated during March, when the natural vegetation has hardly begun to grow. The large clutches are not particularly confined to the urban areas, where the natural food may be augmented by bread, but occur just as frequently in rural areas.

For 67 broods for which the date of the first egg, the number hatched and the number surviving to three months are all known, it is possible to see how the production of young varies with the date of the first egg (Table IV). The number of cygnets hatched is used rather than the number of eggs laid, as egg losses do not depend on the date of laying, but instead to random events such as flooding and human predation. It can be seen that the earliest cygnets survive best. Although the survival rate appears the same for middle and later clutches, more young are actually produced from the early April clutches. This situation holds for many other species (Perrins 1970) and may be explained by relating it to the first few weeks after hatching. As has been shown in an earlier paper (Reynolds 1965), the main mortality in cygnets occurs in the second week after hatching. It was also

Table IV. The production of young with respect to laying date.

Date of first egg	*Number of broods*	*Cygnets hatched*	*Cygnets reared*	*% reared*
up to 31 March	19	135	98	73
1-15 April	30	171	92	54
after 15 April	18	80	45	56

shown that there was a significantly higher survival rate in territories with good surface vegetation, mainly duckweed *Lemna* sp. Presumably in the early summer this provides a conveniently sized food particle for small cygnets, but as the summer progresses, it becomes too large and tangled for any small cygnets then hatched. Thus later broods may have difficulty in finding sufficient food.

Spring weight increases in breeding females

As has been mentioned earlier, breeding females make considerable weight gains just before laying. Unfortunately only four of the breeding females caught at or near their nests during the laying period have been weighed. All were from early April and were up to 2 kg. above normal. Their details are as follows:

Date weighed	Weight (kg.)	1st egg laid
5.4.68	11.7	<15 April
9.4.68	11.3	3 April
9.4.72	11.5	8 April
15.4.68	10.9	c. 4 May

By contrast, one female having completed a clutch of unknown size (due to egg-stealing) by late April weighed only 7.5 kg.

The average weight of 15 eggs, unincubated but at least a day old, was 353 gm. (range 330-390) mostly from early April clutches. The heaviest egg weighed extends the range given in Scott *et al* (1972). Thus females will lay between 1.5 to 4 kg. of eggs depending on clutch and egg size. During the pre-laying and laying period the females spend relatively little time near the nest, but seem to be feeding for most of the time, unless there is a good food source, i.e. bread, close by. Meanwhile the male usually does most of the nest building and guarding of the eggs before incubation begins. The female does most of the incubation. Thus a build-up of the food reserves is necessary for the female to nest as early as possible. Similarly the males need to have sufficient food reserves to enable them to defend the territory and guard the eggs without spending much time feeding.

It is possible to postulate a relationship between the level of a female's food reserves and when laying (or egg formation) is possible. If laying is initiated when the food reserves reach a threshold value, which decreases with time (perhaps governed by day-length), and the clutch size is determined by the food reserves, then the relationship between date and clutch size follows. This is shown diagrammatically in Figure 4 with a fairly arbitrary threshold weight

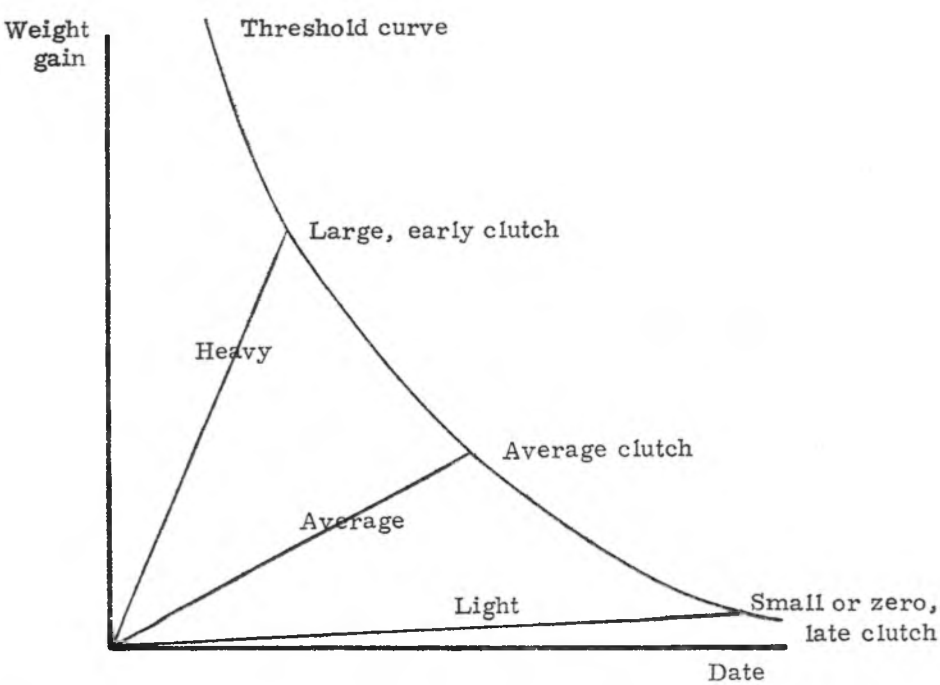

Figure 4. Theoretical diagram to illustrate the gain in weight by a female swan prior to the breeding season, the date of laying and the clutch size.

curve, for three hypothetical birds showing heavy, average and light weight gains.

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Summary

This paper analyses 947 Mute Swan *Cygnus olor* weights, obtained in the Upper Thames valley, with respect to age, sex and season. It was shown for third year or older swans that weights of 10.6 kg. for males and 8.8 kg. for females divided the heavier nesting and territorial birds from the lighter non-breeders. There is a high (negative) correlation between the clutch size and the date of laying of the first egg. The regression line for clutch size on date has a gradient of —1/10 eggs per day, for 120 first clutches (4-11 eggs) started from 15th March to early May. First-time nesting females tended to lay later than previous nesters, and thus had smaller clutches. About 70% of cygnets hatched were reared from early broods (started in March) compared with about 55% from later broods. Females increased their weight by up to at least 2 kg. just before laying. A theoretical model is put forward relating the female's weight, date of laying and the clutch size.

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