Status and dynamics of a Mute Swan population near Oxford between 1976 and 1978

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Introduction

In the late 1950s concern was expressed by some farmers at the (local) damage being caused to their crops by some flocks of Mute Swans *Cygnus olor*, whose numbers, they claimed, were increasing dramatically. This contention initiated a series of national censuses of the species and an intensive ringing campaign sponsored through the Wildfowl Trust. By 1963 in the south of England one swan in four was estimated to carry a ring and in particular areas concerted efforts resulted in proportions of over 90% of breeding birds being ringed (e.g. Perrins & Reynolds 1967; Minton 1968, 1971; Perrins & Ogilvie 1971). Many of these intensive studies have been maintained in subsequent years (e.g. Reynolds 1972; Coleman & Minton 1979, 1980; Bacon 1979a; Ogilvie & Perrins, in press; Hardman 1980) and, in combination with the results of national surveys (Campbell 1960; Eltringham 1963; Ogilvie, in press) are producing a detailed, though complex, view of the status and population dynamics of the species in Britain.

The present paper gives recent data for the 'Oxford' study area of Perrins & Reynolds (1967) and discusses these findings in relation to both the earlier survey and national trends. In brief, the national surveys show that the total numbers of Mute Swans in Britain have changed rather little since 1955, although there have been some dramatic re-distributions: ringing studies show that these re-distributions of numbers, (the most dramatic being the formation and loss of 'urban' flocks), have been brought about by complex dynamic changes in local populations and not by 'mass' dispersals or migrations. This paper is based on data collected during a three year study of the population genetics of Mute Swans (Bacon 1979a), carried out principally in the Oxford study area and concentrating on annual fecundities.

Method

The study area was that of Perrins & Reynolds 1967, and is shown in Figure 1; their local knowledge and extensive records, maintained during the intervening years, greatly facilitated the location of flocks and breeding pairs. A late start to fieldwork in 1976 obliged me to concentrate my efforts that year on the Rivers Thames, Windrush and the lower half of the Cherwell, a sub-area that contained the majority of breeding pairs; within this sub-area each territory was visited about every 10 days to record clutch size, hatching date, number of eggs hatched, and changes in brood size up to fledging (taken as early September). In 1977 the whole area was studied in similar detail and visits to the 1976 study areas were made more frequently; in 1978 additional visits were made to all nests around the expected times of clutch completion, but fewer visits were made that year between hatching and fledging. Infrequent partial surveys were also made in autumn and winter. These surveys, supplemented by observations from local bird watchers provided reasonable data on the locations and numbers of Mute Swan flocks.

Only a few swans were caught for marking from winter flocks, partly because of the emphasis of my main study and partly due to the lack of suitable flocks from which to catch them. However, every effort was made to catch and mark all breeding pairs and all their cygnets. Through the earlier work of C. M. Reynolds and C. M. Perrins most of these breeders were already ringed with a B.T.O. ring and either a colour-combination or an engraved 'Darvic' ring (Ogilvie 1972) and accordingly were probably of known age and origin. Any unringed breeders that could not be identified by sight were captured near the nest; other unringed swans, encountered during my fieldwork were also caught whenever possible. Some additional pairs were ringed by C. M. Reynolds, who also ringed many of the swans which visited the Abingdon flock.

In 1976 and 1977 some pairs and all their cygnets were caught within 7 to 10 days of hatching and the downy cygnets marked

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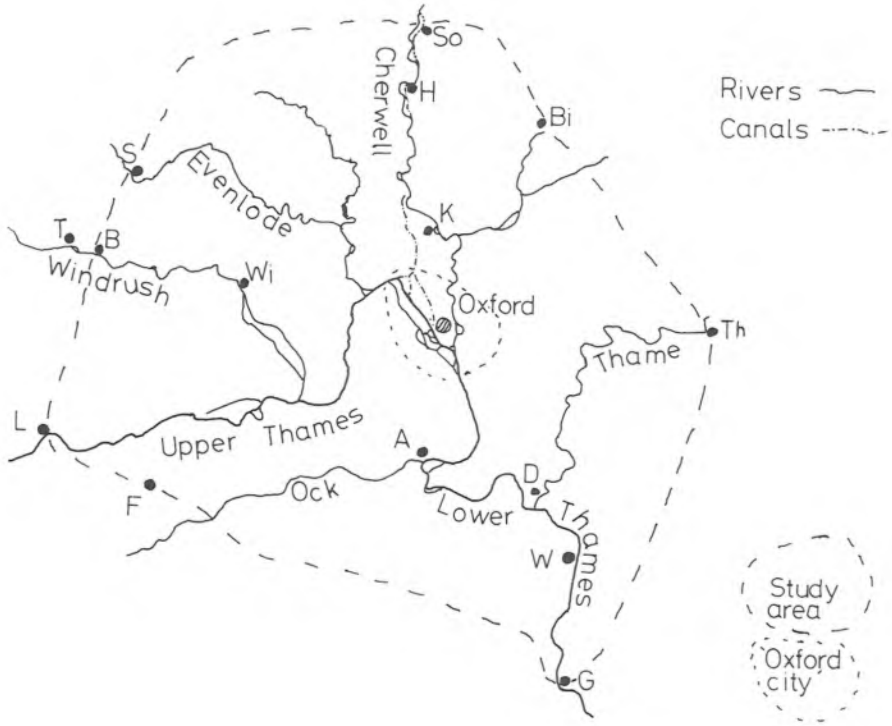

Figure 1. The study area, showing the sub-regions of the river system, the bounds of 'Oxford city', and the study area boundary. Key to towns: So Somerton, H Heyford, Bi Bicester, S Shipton under Wychwood, K Kidlington, T Taynton, B Burford, Wi Witney, O Oxford, Th Thame, L Lechlade, A Abingdon, D Dorchester, F Faringdon, W Wallingford, G Goring.

with small tags fastened to the web of the foot and small spots of a yellow dye (to permit their subsequent individual identification in the field without the need to recapture them). At about 8–12 weeks post-hatching *all* known pairs and *all* their cygnets were caught and marked, if possible (>95% of known pairs). In 1978 families were only caught at 8–12 weeks.

Swans caught for ringing were, whenever possible, sexed by cloacal examination, weighed and measured.

Full details of field surveys and procedures can be found in Bacon 1979a.

Results

Population numbers

The large urban flocks, numbering well over a hundred birds, that typified the area in the 1960s have completely gone. Only groups of a dozen or so (rarely more than 20) are now found in the city of Oxford and similarly small numbers now summer in Abingdon. Winter flock numbers in Oxford are also low (20–30), though numbers in Abingdon may go up to thirty, mainly on the edge of the town and now rarely staying for much of the winter.

Groups of a dozen or so moult on a few of the gravel pits in the area, and the non-breeding summer total is probably around 150. In winter this number increases to around 450–500. It is thought that most of these birds move into the study area from: (i) the new gravel pits between the headwaters of the Thames and Windrush, west of the study area boundary (new = dug since 1967) (c. 120) (ii) the Thames below Goring (50–100) (iii) the headwaters of the Cherwell (c. 50) (iv) the headwaters of the Thame (c. 30).

Immigrants

In the past a few birds ringed on the lower reaches of the Thames have moved upstream into the study area (30 plus from the flock at Reading and smaller numbers from elsewhere; C. M. Reynolds, pers. com.). During the current study four birds ringed in or around Stratford were located; three of these were territorial (two breeding) and the fourth an immature who died from lead poisoning.

Breeding densities

About 80% of pairs in the Oxford study area nest along river systems, and territories can be usefully defined as 'kilometres of river'. Such data are presented in Tables 1 and 2 for the sub-regions shown on the map in Figure 1. It should be noted that the lengths of river include, where appropriate, backwaters and weir streams. It can be seen that there is considerable variation in territory length between the river systems, and in Table 2 these values are compared with Eltringham's (1966) for the Thames/Kennet, as compiled by aerial survey. It can be clearly seen that the Windrush, which is a highly productive trout stream with rich aquatic vegetation, had densities between two and eight times those elsewhere: in contrast the Thames is excessively deep, and boat traffic on the Thames, greatly increased since the 1960s, reduces the submerged vegetation available to swans, while bank erosion caused by the wash makes it difficult for swans to walk out and graze surrounding meadows. Similarly, much of the Evenlode is shallow and fast flowing with frequent ripple patches and high banks, these attributes combining to give generally poor water-weed growth, although it is luxurient in patches. Table 3 compares the nesting densities found in 1976–1978 with earlier values (Perrins & Reynolds 1967; Reynolds 1971, and pers. com.). It should be noted that densities of breeding pairs have declined dramatically (to c. 40%) on both sections of the Thames and within Oxford. In contrast, the number of pairs on the Windrush has nearly doubled since 1965. However, the Windrush was heavily dredged in 1965 (C. M. Reynolds, pers. com.), and re-dredging of its lower half in 1979 drastically reduced nesting densities on that stretch (Scott & Birkhead 1979; pers. obs.).

Table 2. Lengths of river per breeding pair, 1976–1978, with comparable data for other river systems from Eltringham (1962).

	Kilometres of river per breeding pair			
River system	1962	1976	1977	1978
Windrush		2·1	2·4	2·0
Cherwell		—	5·3	5·3
Evenlode		—	8·3	17·0
Upper Thames		4·0	5·0	6·6
Lower Thames		6·7	16·7	16·7
Thame		—	7·7	7·7
Oxford		—	2·8	3·6
Severn	4·8			
Thames/Kennet	3·7			
Wilts/Hants	3·2			

The data are adjusted by the length of each river surveyed in detail each year and are accordingly directly comparable (unlike the data in Table 1).

Laying dates and clutch sizes

Reynolds (1972) showed that the clutch

Table 1. Territorial (T) and breeding (B) pairs on sections of the Oxford study area, showing numbers of pairs and length of rivers.

	Total length	Number of pairs					
		1976		1977		1978	
River	km	T	B	T	B	T	B
Windrush	39	>12	>11	>14	>13	20	19
Cherwell	32	≫ 3	≫ 3	7	6	7	6
Evenlode	32	—	—	5	4	5	2
Upper Thames	40	12	10	10	8	7	6
Lower Thames	46	11	7	6	3	4	3
Thame	37	—	—	8	5	9	5
Oxford	36	12	>10	14	13	11	10
Other sites	—						6

The data refer to sections surveyed in detail only (see text and Bacon 1979a for details of rivers included). Data for 1977 is almost complete. Comparison with BTO census data for 1978 show 7 territorial pairs, 1 breeding, not included in my survey for that year. These were largely (5/7) on 'Other' sites.

Table 3. Estimated totals of territorial non-breeders and breeding pairs for seven river sub-areas around Oxford, with the river sub-totals and estimated grand-total, for different years since 1956.

	Estimated totals of territorial non-breeders and breeding pairs											
	Year											
River system	56	64	65	66	67	68	69	70	71	76	77	78
Windrush	6			9	12	10	11			12	14	20
Cherwell	10		7	8	11	9	7				7	7
Evenlode											5	5
Upper Thames	8			12	12	15				12	10	7
Lower Thames	11		13	16	17	13	11			11	6	4
Thame	11			8	8	8					8	8
Oxford	14	17	12	21	19	17	13			12	14	11
Est. river total	60			76	79	70	58			—	64	63
Est. grand total	c 100		120	100	100	103	86	80	86	72	70	76

N.B. Breeding pairs are always territorial. Data for 1956–1971 from Reynolds, unpublished.

size of the Mute Swan declines, almost linearly, with the date of clutch commencement: this correlation was evident from my own data in all years ($p < 0{\cdot}001$). However, my visits to each nest site were frequent and systematic which enables me to elaborate on the following points. First, eggs are not invariably laid at 48-hour intervals; both longer and shorter periods may be observed (confirmed by Dr J. R. Baker and C. M. Reynolds, pers. com.); for this reason it is necessary to visit all nests frequently to determine accurately the date of initial laying. Second, a few females may lay an initial egg on the bank, or in last year's nest, and then abandon it (occasionally them): it is thought that spells of severe weather may promote this anomalous behaviour and some cases of irregular laying intervals, but data are too few to investigate this.

Figure 2 gives histograms of laying dates (in ten-day intervals) and final clutch sizes for both 1977 and 1978. In both years clutches known to have been completely or partially predated (predation is almost entirely by humans) have been omitted from the clutch size data. The distribution of clutch sizes are not significantly different between the years ($p > 0{\cdot}20$), but those of laying dates are ($p < 0{\cdot}05$); the main difference in the distribution of laying dates is in their spread, the variances differing by a factor of nearly two ($p < 0{\cdot}02$) although the means are indistinguishable ($p > 0{\cdot}35$). April 1978 was 'the coldest on national record': this fact, combined with the observation that females on the Windrush laid significantly earlier than those of other sub-regions in 1978 (one-tailed $p = 0{\cdot}039$) but not in 1977 ($p > 0{\cdot}20$), plus the generally late laying dates following the severe 1978–1979 winter, both around Oxford (Scott & Birkhead 1979) and elsewhere (Coleman 1979), show that laying dates can vary between seasons and habitats. It is possible that clutch sizes show similar real variation with these factors, but the discrete nature of this variable and the small sample sizes would make this hard to prove. In addition, laying dates around Oxford vary significantly depending on the genotype of the female, and clutch sizes depending on the genotype of her mate (both male and female genotypes defined by allozymes at a locus for esterases, isolated from samples of plasma). This observation greatly complicates any overall analysis of factors affecting clutch size, and is discussed in detail elsewhere (Bacon 1979a).

Hatching and fledging success

The most comprehensive records were obtained in 1977 for the rivers Windrush, Cherwell and 'Oxford city' complex. These are based on 10-day, or more frequent, visits to all territories, with brood size data supplemented by observations from reliable local observers. The data are presented in Table 4, which shows percentage mortality (i) from various causes during incubation and (ii) in weekly intervals during fledging. The greatest losses during incubation are from (human) predation, with flooding being the other major factor. The frequency of flooding varies between seasons and river systems and pairs on the Thame are particularly at risk from flooding. During fledging the high losses occurring immediately post-hatching are thought to be deaths of cygnets that were 'weaklings'. Thereafter mortality is around 6% for the next two or three weeks, and around 2% for weeks 4 to 8. The different mortality figures discernable for each area probably arise from genuine factors: (human) predation will be higher in urban areas (interference from fishermen and game-keepers, frequently recorded by Reynolds in the 1960s, was not common during my study), while the burst of mortality around week 3 coincided with a period of heavy rain when many cygnets were lost. Some of these losses would represent deaths due to exposure, but

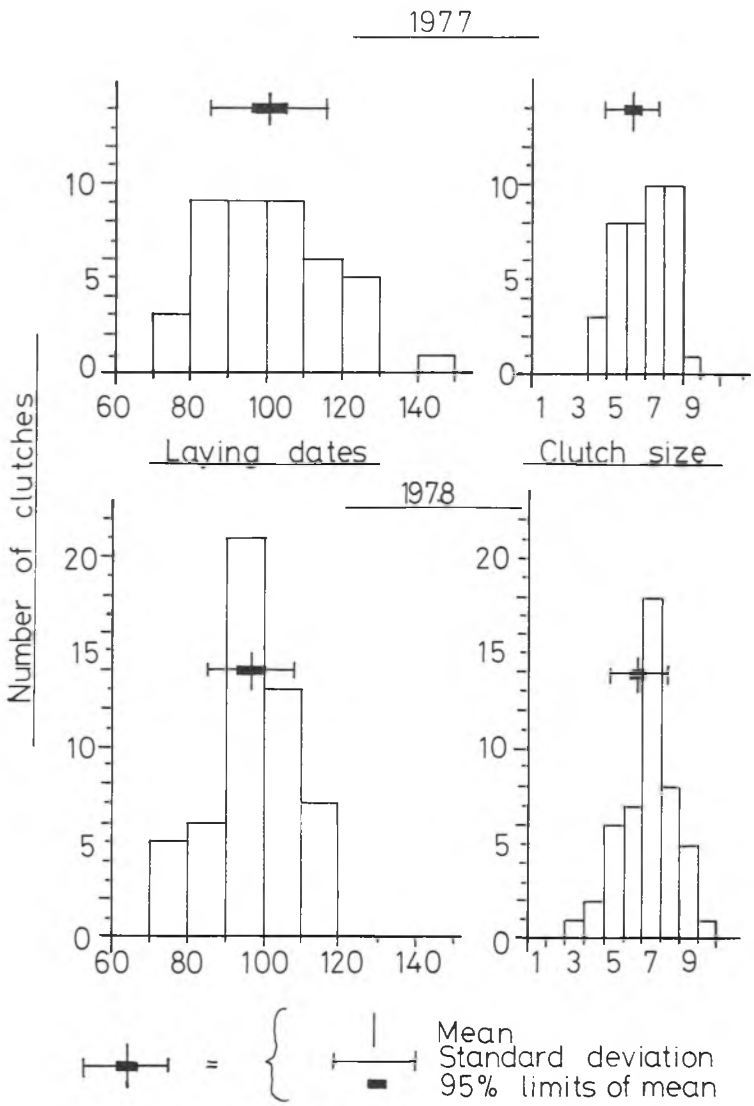

Figure 2. Histograms of (i) laying dates of first eggs of first clutches, and (ii) final clutch size, for completed clutches only, for 1977 and 1978. The mean values and 95% limits shown are, for laying date: 1977, 100·4 ± 4·8, and 1978, 97·0 ± 3·3; and for clutch size: 1977, 6·45 ± 0·42, and 1978, 6·72 ± 0·44. Dates are from 1 Jan = day 1.

Table 4. Mute Swan productivity in 1977.

Category	Cause of loss	Windrush 13/13* No.	%	Oxford 12/13 No.	%	Cherwell 5/6 No.	%	1977 Sub-total 30/32 No.	%
Eggs laid		77		75		32		184	
	Flooded		0·0		12·0		0·0		4·9
		77		66		32		175	
	Predated		16·8		33·3		0·0		20·0
		64		44		32		140	
	Other		0·0		0·0		0·0		0·0
Eggs left to hatch		64		44		32		140	
	Not hatching		12·5		4·5		18·7		11·4
Hatched eggs		56		42		26		124	
	Weakling		1·8		4·8		11·5		4·8
Left nest		55		40		23		118	
			5·4		25·0		4·3		11·9
Survived	1 week	52		30		22		104	
			3·8		13·3		4·5		6·7
	2 weeks	50		26	21	97			
			4·0		0·0		9·5		4·1
	3 weeks	48		26		19		93	
			10·4		7·7		10·5		9·7
	4 weeks	43		24		17		84	
			0·0		0·0		5·9		1·2
	5 weeks	43		24		16		83	
			2·3		0·0		0·0		1·2
	6 weeks	42		24	16	82			
			9·5		8·3		0·0		7·3
	7 weeks	38		22		16		76	
			0·0		0·0		0·0		0·0
	8 weeks	38		22		16		76	

* n_1/n_2 n_1 = pairs with detailed records
n_2 = total pairs breeding

downy cygnets are very prone to being washed over weirs and separated from their families: this happened to some marked individuals in 1977, whose subsequent fates could be followed. If separated cygnets are lucky, and less than 10–20 days old, they may be accepted into, and reared by, the next family downstream. This happened on two occasions in 1977. Cygnets may also change broods during territorial disputes, cygnets from the vanquished pair being adopted by, or adopting, the victorious pair. Such instances are by no means exceptional. Many lock keepers on the Thames have witnessed similar cases of 'adoption' over the years, and a frequency of 1–3% would seem typical. Minton (1968) and C. M. Reynolds (pers. com.) have also recorded such adoptions. Downy cygnets washed over weirs and not adopted almost certainly die: however, cygnets more than a month old on separation may survive as lone orphans; two of five orphans survived to 8 weeks age in 1977 (total cygnets surviving at 8 weeks that year was 131). If cygnets missing from a brood could not be found during a census transect they were presumed dead. However, lone orphans generally become very secretive, and one of four orphans web-tagged in 1977 and presumed dead after exhaustive searching, was subsequently recovered alive and healthy in April 1978.

Table 4 contains data for only the most intensively studied areas, for which weekly mortalities could be accurately given. Table 5 compares the former data with less exact information for other sub-regions for the same year, and also for those sub-regions studied in 1976. The general patterns are much the same and were broadly similar in 1978 also. In 1977 a census of most broods at around 12 weeks of age showed no mortality had occurred during weeks 8–12.

Table 6 shows the numbers of cygnets reared to fledging in the different sub-regions of the study area. The high proportion of total cygnets fledging from the short stretch of the Windrush should be noted.

Mortality post-fledging

Broods of Mute Swans may wander considerably after September and begin to fragment, so censuses of territories no lon-

Table 5. Productivity and losses, comparing data from Table 4 with less exact information for other sub-regions in 1977 and in 1976. Tabulated values are % losses between stages.

Life stage	Cause of loss	Coarse data 19/23*	1977 Weekly data 30/32	Total data 49/55	1977 Total data 49/55	1976 Total data 21 pairs
Eggs laid	Flooding	10	5	7	7	0
	Predation	20	20	20	20	7
	Other	21	0	7	7	3
Eggs left		6	11	9	9	12
Eggs hatched	Weakling	12	5	7	16	12
Weeks 0–1		33	36	35		
Weeks 1–8					30	15
Weeks 8–12		—	—	0	0	—

* See note to Table 4.

Table 6. Breeding success in sub-regions of the Oxford study area in two years. The totals for 1978 are nearly complete; 'other' areas not so comprehensively surveyed in 1977.

1977	No. pairs	No. eggs	Eggs per pair	No. fledged	Fledged per pair
Windrush	13	84	6·5	38	2·9
Oxford	9	59	6·5	22	2·4
Cherwell	5	34	6·8	14	2·8
Evenlode	4	27	6·7	14	3·5
Upper Thames	7	44	6·3	2	0·3
Lower Thames	2	12	6·0	7	3·5
Thame	2	11	5·5	7	3·5
Total ex. Windrush	29	187	6·4	66	2·3
Grand Total*	42	271	6·4	104	2·5
1978					
Windrush	19	132	6·9	78	4·1
Oxford	8	53	6·6	20	2·5
Cherwell	6	39	6·5	24	4·0
Evenlode	2	9	4·5	3	1·5
Upper Thames	3	16	5·3	12	4·0
Lower Thames	1	8	8	1	1
Thame	4	29	7·2	0	0·0
Other*	3	22	7·3	5	1·7
Total ex. Windrush	27	176	6·5	65	2·4
Grand Total*	46	308	6·7	143	3·1
Uncertain/missed†	12			40	
1978 estimate‡	58			183	
Windrush	33% pairs		42% fledged cygnets		
Other	67%		58%		

*, †: see text Table 1A and Bacon 1979a for details of areas surveyed; ‡—estimated from national census returns and Reynolds (pers. com.) and refering to the WHOLE study area.

ger give comprehensive, reliable totals. During a local three year study sample sizes of swans recovered dead are too small to give accurate mortality estimates, but can be used as a guide. The recovery rate at death for British Mute Swans was given as 33% by Perrins (1980), from the national ringing data. Using a 33% recovery probability at death and the numbers of cygnets reported dead during my own study give the following values:

Cygnets hatched in 1976 suffered a 30·5% mortality between October and July of their first year and a further 29·0% in their second year (July to July). In their first year, 1977 cygnets had a mortality 28·0%: these estimates are regrettably imprecise, but the best possible.

Adult mortality

During the study five breeding adults of my intensively studied pairs were recovered at death via the national ringing scheme, indicating a 15% annual mortality. This sample size is extremely small however, and fortunately an independent estimate can be made. Breeding pairs are extremely likely to re-nest on the same, or nearby, territories in successive years; if they survive from one year to another they are almost certain to be re-sighted during census surveys. I surveyed some 30 pairs in detail in 1976 and 55 in 1977. Of these, 24 to 30 birds (likely maximum 34) did not return in subsequent years, nor were they subsequently seen elsewhere. Taking a total of

Table 7. Life-table for Mute Swans of the Oxford area, comparing previous and recent findings.

	Current study, Bacon 1979a		Perrins & Reynolds (1967)
Each pair lays	6·60 eggs		6·00
		5% flooded	
	6·25 eggs		
		20% predated	
	5·01 eggs		
		7% unknown	
Each pair retains	4·66 eggs		
		9% don't hatch	
Each pair hatches	4·25 cygnets		4·00
Each pair raises	4·06 cygnets to 3 days		
		5% 'weaklings'	
		12% 1st week losses	
Each pair raises	3·54 cygnets to 10 days		
		7% 2nd week losses	
		6% 3rd week losses	
		6% 4th week losses	
		6% 5th week losses	
		6% 6th week losses	
		6% 7th week losses	
Each pair raises	2·30 cygnets to 8 weeks		
		2% losses/week	
Each pair fledges	2·26 cygnets at 12 weeks age		2·00
		30% losses until age 1 year	
Each pair attains	1·58 survivors to 1 year		1·30
		30% second year losses	
Each pair attains	1·10 survivors to 2 years		0·89
		c. 25% third year losses	
Each pair attains	0·82 survivors to 3 years		0·67
		c. 25% fourth year losses	
Each pair attains	0·62 survivors/brood to breeding age		0·43
Adult mortality	$(2 \times 0{\cdot}20) = 0{\cdot}40$ adults die/pair/year		

Summary	Observed values, Bacon, 1976–1978			Published data, Perrins & Reynolds
Summary	Min.	Mean	Max.	1967
Credit from cygnet production	0·57	0·62	0·88	0·43
Debit from adult losses		0·40		0·36
Balance per pair per year	0·17	0·22	0·48	0·07

$2 \times (30 + 55)$ adult years, the loss of 24–30 (34) indicate annual mortalities of 14%–18% (20%). This mortality estimate is close to those of Perrins & Reynolds 1967 and Minton 1968.

The fecundity and mortality data may usefully be summarized in a life-table, and Table 7 compares my own data with that of Perrins & Reynolds 1967 in this format.

Biometrics

Egg volumes

During 1977 and 1978 detailed investigations into egg volumes were made, since it seemed possible that this variable might be affected by genotype. A detailed analysis would need to assess effects of season, habitat, female age and genotype and cannot be realistically undertaken with present sample sizes because current results show that, in contrast to some avian species (e.g. Davis 1975; Parsons 1970), variation of Mute Swan egg volumes are not likely to have major effects on hatching or cygnet survival, either within or between broods.

Cygnet growth

In 1976 cygnets reared on the Windrush tended to be heavier than those reared elsewhere in the study area, both shortly after hatching and near fledging. The combined results that year suggested growth was linear between 15 and 60 days, and that weights could therefore be reliably interpolated for standard ages (it was not practicable to catch all broods at the same age). Figure 3 shows these data, contrasting the weights of Windrush and Thames cygnets. The variation in weights between

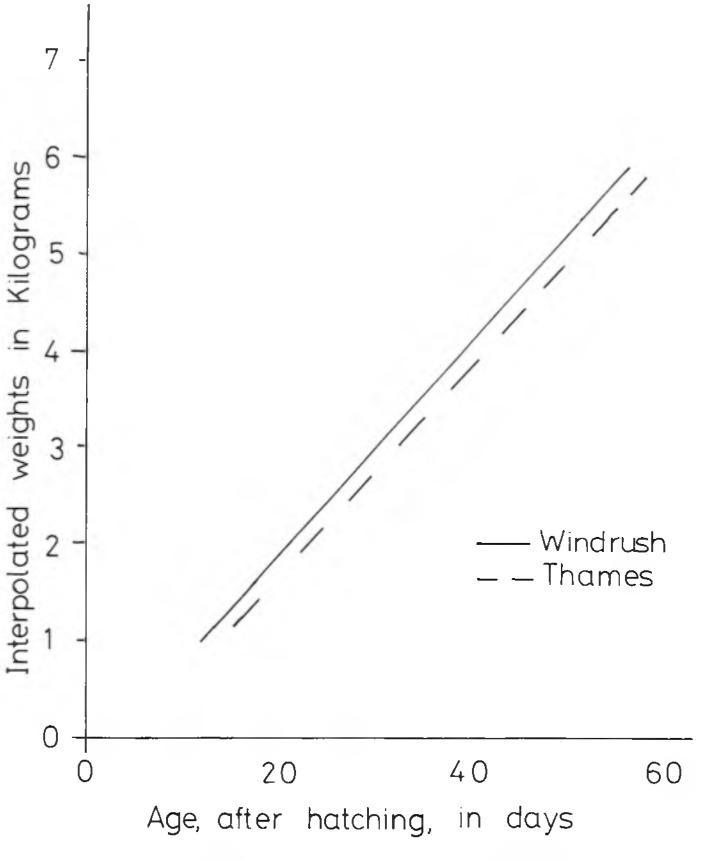

Figure 3. Growth of cygnets in 1976, contrasting broods on the Windrush and the Thames. Plotted weights are interpolated to standard ages for comparison; growth was linear over this age for all broods in 1976.

individuals of a given age is very considerable; the difference between the average weights for the two areas is not at all significant. Sexual dimorphism, apparent from an early age, accounts for a large, unknown, proportion of the weight variation, but food supply, itself probably affected by habitat and season, is probably important. Growth rates of individual cygnets can vary widely in similar habitats; in 1976 two cygnets comprising a very late re-laid clutch on the Windrush had attained almost the heaviest weights on the river that year.

In 1977, a spell of poor weather caused a general drop in growth for many broods and thus prevented reliable weight estimates for standard ages. I concluded (Bacon 1979a) first, that adequate growth curves could only be constructed by weighing sexed cygnets every 10 days or so; second, that such a frequency of capture, to obtain the weights, would be seriously detrimental to broods of Mute Swans. Since mortality in this period is generally low, such disturbance would seem unwarranted.

Adult weights

The weights of fledged cygnets, immatures and breeding adults were consistent with the findings of Reynolds (1972) for the same area.

Discussion

Minton (1972) showed that the number of swans in April non-breeding flocks in south Staffordshire dropped from about 400 in 1962 to about 200 in 1968; since then, numbers have remained similar (200), or declined slightly. During the 1960s and 1970s the number of pairs, including non-breeders, has fluctuated, but remained much more constant (Minton 1972; Coleman & Minton 1980, & pers. com.), ranging between 152 and 220 birds: these pairs have produced fluctuating numbers of cygnets each year (75–170), but there has similarly been no overriding trend in production with time. There has, however, been a noticable loss of breeding pairs from urban areas during this period (A. E. Coleman, pers. com.).

Data for the Oxford area are less comprehensive, but show a similar pattern: numbers in non-breeding flocks in the 1960s exceeded those of breeding pairs by a similar factor (c. x2; Campbell 1960) but have now declined to a number similar to or lower than that of breeding pairs. However, in contrast to the trend in south Staffordshire, my data suggest that breeding numbers around Oxford have declined from c. 100 pairs in the early 1960s, to 70–80 breeding pairs in 1976–1978: this would represent a decrease to about 70% of former levels. The long term data for south Staffordshire shows a decrease in breeding pairs of some 18% during 1976–1978 (A. E. Coleman, pers. com.), so some of the decrease in the Oxford area may be part of a general trend. However, reference to Table 1 clearly indicates that the declines have been localized in the Oxford area, being approximately 20–12 in 'Oxford', 15–6 on Lower Thames, 12–8 on Upper Thames sub-regions. For the same period numbers in the sub-regions Thame and Cherwell have remained very similar, while they have nearly doubled on the Windrush, 9–18, though the recent dredging of the Windrush has suddenly altered the overall picture. Most of the losses of breeding pairs from Oxford, the Upper and the Lower reaches of the Thames, represent traditional territories that have now been consistently vacant for years. This suggests that local factors have made conditions unsuitable for breeding attempts. Many adults pass through these areas each spring, but do not choose to settle and attempt breeding; indeed these stretches are often devoid even of territorial non-breeders throughout the summer. It is noteworthy that, within the Oxford area, increased leisure activities from boating and fishing have occurred predominately in those sub-regions where large decreases in breeding numbers have taken place. I personally regard much of these sub-regions as being (currently) unsuitable breeding habitat for Mute Swans, rather than areas of suitable breeding habitat that are unfilled due to low population density.

On the subject of suitable breeding habitat, I disagree with the suggestion by Perrins & Reynolds 1967 that '. . . if . . . a site which is occupied in one year is a suitable nesting site, then we have more suitable nesting sites than we have pairs of swans'. This definition does not seem to me to be a useful description of suitable nesting habitat. I have speculated elsewhere (Bacon 1979b) that in the early 1960s the high densities of mature swans greatly exceeded the number of suitable territories, obliging mature birds to attempt breeding in marginal areas with much lower chances of success. In the 1960s the population in the Oxford area was in approximate equilibrium and Reynolds' data (1965) show that pairs in 'good' habitat had significantly better fledging success than pairs in 'poor' areas, fledging 64% versus 28% of hatched cygnets respectively ($p < 0{\cdot}01$). This clearly indicates that a 'population' restricted to poor habitat could not maintain itself and also that there would be a very strong selective advantage in favour of breeding in 'good' areas. I therefore suggest that in the early 1960s around Oxford several pairs bred in marginal habitat, where they fledged some cygnets, but insufficient to outweigh their own mortalities. I recognize that by breeding they would increase the overall productivity of the population and also decrease their own mortality; however, individuals would be selected against if they continued to breed in marginal areas when better quality habitat became available. By 1976–1978 these 'former territories' had presumably become unfavourable in the prevailing conditions of reduced competition for nest sites from an overall lower density of pairs. However, the hypothesis must remain speculative because overall territory quality has declined in these areas between 1960s and late 1970s. I note that Reynolds (1965) found duckweed *Lemna* sp. characteristic of good nesting habitat; during my study this water weed was not a prominant part of the flora.

Perrins & Reynolds (1967) pointed to the difficulty of obtaining accurate clutch size data for Mute Swans due to humans removing an egg or two from partly completed clutches. Unless visits to nests are extremely frequent, such predation will be undetected and a falsely low clutch size will be recorded. Perrins & Reynolds also recognized this limitation might produce a slight low bias in their clutch size data. Conversely, Reynolds (1972) noted an upward bias in the mean clutch size (7·5) for the data used in his regression calculations due to the over-representation of large early clutches. My own data for both 1977 and 1978 were systematic, visits to all sites were frequent for a wide, comprehensive range of habitats (my records slightly under-represent gravel pits and lakes, but the data I have for these sites are closely similar for both clutch sizes and laying dates to nests in riverine areas), and my data also include a higher proportion of rural nests, where the frequency of (human) predation was low and the overall bias from predated eggs likely to be smaller. As my overall average clutch size of 6·6 eggs was similar in both 1977 and 1978, and is higher than that of 6·0 noted by Perrins & Reynolds (1967) I would suggest that 6·6 is a closer approximation to the average 'intended' clutch size for Mute Swans around Oxford. I would attribute the difference between our findings (about 0·6 eggs/clutch) entirely to differences in recording methods, though possibly modified slightly by (i) differences in the proportions of habitats regularly surveyed and (ii) seasonal differences. I would *not* suggest that mean clutches were generally smaller in the 1960s than in 1976–1978.

My data show significant seasonal and regional variation in mean laying dates, and corresponding, but non-significant, differences in mean clutch sizes. It is tempting to infer from the known regression between these variates that the clutch size differences are also 'real' (non-significant due to the discrete variation); however, our knowledge of cause and effect is too poor to justify this inference, and the regression parameters themselves may be subject to seasonal variation. It seems likely that these differences, and possibly the genotypic effects mentioned earlier, are caused by seasonal and habitat variation in, and genotypic preference for, the quality and quantity of food (soft-water weeds?) available to females in early spring when they are forming eggs (Bacon 1979a; see also Reynolds 1972). I specify elsewhere (Bacon 1979a) the data necessary to investigate these complex interactions; such investigation would require large sample sizes for an extended period to show statistically significant effects.

There is an apparent discrepancy in net productivities between my own data and that of Perrins & Reynolds 1967 (see Table 7). The life-history data is shown simplified in Table 8 and from this it can be seen that a very minor adjustment to the mortality at one stage (4%, well within observational accuracy) almost entirely removes the difference between our mortality estimates. The difference in productivity would similarly vanish if my mean clutch size of 6·6 was substituted for theirs of 6·0. I would also suggest that the differences in the timing of mortality in downy cygnets between our results is a seasonal effect and that it is accordingly not necessary to invoke depletion of yolk reserves, resorbed from the egg, to explain the mortality pattern observed by Reynolds (1965). My own data indicate different mortality patterns in different years, due to severe rain storms, and Reynolds (1965) mentions rain as a possible cause of his own peak losses (based on data for a single season). Finally, to emphasize that the differences in cygnet productivity between our results are small, I present in Table 9 the means and annual variations in cygnets fledged/breeding pair for five different areas of Britain. The difference between my own data and the results of Perrins & Reynolds are clearly small compared with expected seasonal differences. Unfortunately, such small differences in fecundity and mortality estimates may produce large differences in the overall population dynamics.

Lastly, by way of contrast, Table 8 also includes data taken from Coleman & Minton (1980), which are based on continuous surveys and large sample sizes. In comparison with the Oxford data a radically different mortality pattern is evident, with approximately half the overall survival probability from egg (1st clutch) to breeding adult. Egg predation is so frequent in south Staffordshire that clutch sizes cannot be reliably recorded, so we cannot estimate net productivity for south Staffordshire

Table 8. Simplified Life-table for swan pairs around Oxford in two studies and (1) the results of one study adjusted (2) compared with another area.

	Observed values from different studies (ratios between these)					
					(1)	(2)
Production or Mortality stages	P & R 1967	Bacon P & R 67	Bacon 1979	Bacon P & R ad.	P & R adjusted	Coleman & Minton 1980
1 Incubation	0·67	(0·95)	0·64	(0·95)	0·67	0·51
2 Fledging	0·50	(1·06)	0·53	(0·98)	0·54*	0·76
3 Immaturity	0·21	(1·29)	0·27	(1·08)	0·25	0·12
4 Overall pre-breeding survival	0·07	(1·19)	0·09	(1·00)	0·09	0·045
5 Egg production	6·0	(1·10)	6·6	(1·10)	6·0	
6 Annual change	0·42	(1·45)	0·62	(1·15)	0·54	
7 Adult losses per pair	0·36		0·36		0·36	
8 Net change per annum	+0·06		+0·26		+0·18	

1, 2, 3 Observed survival probabilities
4 = 1 × 2 × 3 = survival probability to breeding age
5 = Observed mean clutch size (first clutches)
6 = 4 × 5 = mean survivors per clutch to breeding age
7 = twice adult mortality = losses/pair/year
8 = 6 − 7 = intrinsic annual population growth factor, r.

0·54* is the only adjusted value in the basic data; see text. P & R are the results of Perrins & Reynolds 1967; the Bracketed figures are the ratios of my results to theirs.

Table 9. Expected annual variation in number of cygnets fledged per breeding pair for five sites in Britain.

	Study area	Number of years	Cygnets fledged Mean		S.D.	c.v.	95% confidence limits	95% c.l. as percent mean
a	Oxford	11	2·24	±	0·58	26%	1·29	58%
b	South Staffs.	18	1·84	±	0·35	19%	0·75	40%
c	Uists	4	1·37	±	0·62	45%	1·72	125%
d	Radipole	10	2·20	±	0·75	34%	1·67	76%
d	Abbotsbury	10	1·60	±	0·92	57%	2·05	128%

S.D. = standard deviation (of a single year's data about the mean)
c.v. = coefficient of variation = S.D./Mean
95% confidence limits: the range on either side of the mean, adjusted for sample size (n years), within which 95% of all annual values are expected.
(a) Reynolds (1971 and pers. comm.). (b) Coleman & Minton (1980 and pers. comm.). (c) Jenkins *et al.* (1976). (d) Ogilvie and Perrins (in press).

directly. However, assuming a mean annual mortality for breeding adults of 15% (derived from Minton (1968)) we may calculate that swans in south Staffordshire would need an average clutch size of 6·7 to attain a stable population: the required mean clutch size can be calculated as 2·9 to 10·2 if Minton's minimum and maximum adult mortalities are used instead. The 'required mean clutch size' for Oxford swans is, for comparison, 4·5. These calculations support my subjective impression that swans in the Oxford area currently have a slight excess of cygnet production over adult losses, whereas south Staffordshire probably has a slight net deficit. I presume the excess birds disperse out of the Oxford area; 20% of cygnets reared in the Oxford area are recovered outside it (C. M. Reynolds, pers. com.); some of those may remain away, others might return and breed (e.g. Coleman & Minton 1979). Mortality of mature breeding Mute Swans clearly needs to be known with great accuracy before net population changes can be adequately estimated, due to the large effects of a small percentage error over a long generation time (approximately 8 years; see Bacon 1979a).

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Summary

During 1976–1978 a study of the population genetics of Mute Swans *Cygnus olor* was carried out, concentrating on a population near Oxford. The population dynamics of swans in the Oxford study area during that period are recorded and compared to earlier findings and similar studies elsewhere in Britain. The density of non-breeders and breeding pairs is lower overall; the distribution of breeding pairs has altered, both local decreases and local increases are apparant; cygnet production per pair may be slightly higher, but the observed change in this is within expected seasonal variations. The overall production of cygnets in the area may now depend largely on a few small areas of 'good' habitat.

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A brood of Mute Swans *Cygnus olor* being herded prior to capture for ringing. (*Douglas Fisher Production Ltd.*)