

SECTION 2: POPULATION STUDIES

Survival rates of young Mute Swans *Cygnus olor*



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The ringing and recovery data from the British Trust for Ornithology have been computerized and the following analysis made, with special emphasis on the survival rates of birds of known age (those ringed in their first 15 months of life). On average, slightly over one in four of the swans ringed in Britain are eventually reported dead. Analyses based on this reporting rate are presented showing the total number of deaths in any time period and in any area and, resulting from this, the 'pool' of birds still alive from which the recoveries have come.

The pattern of mortality within the first year of life is examined and compared between areas within Britain. The pattern seems to be largely similar over the whole country. Mortality rises sharply in October when birds begin to leave their natal territories and remains high during the winter months but drops again in April as the birds settle down to spend the summer in an area where they eventually moult. Survival rates of the one year old cohort are followed through their first seven years of life, by which time they should be of breeding age. Comparisons are made between areas within Britain and over different time periods.

The aim of this paper is to use the data on the ringing and recoveries of young Mute Swans *Cygnus olor* in Britain to establish a picture of their survival during their first year. Although the results seem sensible, they are based on the assumption that the reporting rate of swans dying at different times of year does not vary. This cannot be tested and so must remain a possible source of error.

Patterns of survival rates of young birds, especially those in their first year, are difficult to estimate for a number of reasons. First, people making intensive, but local, population studies cannot easily make such estimates because young birds commonly disperse widely after becoming independent. In addition, questions are inevitably asked about the general applicability of a local study. Second, although ringing data cover a much wider area, these have not, as yet, proved very useful for measuring the survival rates of young birds; the estimation of survival rates within the first year is not easily done by conventional analyses of ringing recoveries (e.g. Brownie *et al.* 1985). Hence survival rates of newly fledged young have not often been measured directly, though sometimes they have been measured by indirect means, such as changes in juvenile : adult ratios with time (e.g. Lack 1951). Looking at the

recovery rates in relation to the numbers ringed has seldom been attempted in Britain because of the labour involved in extracting the ringing data for any single species from the ringing schedules.

The Mute Swan presents an unusual case. Since only a few other species are ringed with the same size of ring as the Mute Swan, it proved relatively easy to go through the ringing schedules at the British Trust for Ornithology (B.T.O.) and to extract the ringing data for this species. In addition, a high proportion of the ringed birds are subsequently found dead by members of the public and reported. I have used these two facts to produce an estimate of the pattern of mortality in young Mute Swans, from the stage at which they become large enough to ring (i.e. the age of about ten weeks) through to adulthood.

Methods

The data used here are for Mute Swans ringed in Britain and Ireland until the end of 1988 and also the recoveries of any reported up until the end of 1988. I have narrowed the data set so as to use only those birds ringed as cygnets (a cohort of cygnets is ringed from July in its year

of birth to September in the following year when the young birds cease to be recognisable as belonging to that cohort). All cohorts have been lumped for some of the main analyses, though they are subdivided by time periods, cohorts and geographical regions for other analyses.

The calculations made are based on the idea that it is possible to calculate from the ringing recoveries the total number of birds that died each month and, by subtracting these from the number ringed, to know the number remaining as a "pool" of ringed birds that were alive the following month. To do this, it is necessary to know what proportion of the birds which die are found and reported and to "correct" the actual reporting rate to obtain the total number of deaths. In order to do this, I first looked at birds that were ringed before 1975 and had been recovered by 1987 (for this analysis, all ringed swans, not just the cygnets, were used). Since rather few swans survive for more than twelve years, this should give the proportion of dead birds that are reported. The results are shown in Table 1 and are compared with those for birds ringed before 1970 and before 1965 and recovered by 1987; any birds still alive from these periods would be, respectively, over 17 and over 22 years of age. As can be seen, the percentage of the birds reported is remarkably similar, the percentage is not increased by taking older birds into account (though note that the three periods include birds in common). Hence, any bias produced by birds which were, in fact, still alive seems to have been negligible. In all some 26.5% or 1 in 3.77 swans which die are reported to the BTO.

Table 1. The percentage of ringed Mute Swans reported dead by the end of 1987.

Ringed up to:	1965	1970	1975
No ringed.	14,030	20,897	26,552
No. reported dead	3,713	5,594	7,048
% reported dead	26.5	26.8	26.5

It is the key assumption of this paper that, by multiplying the number of *deaths reported* in any month by 3.77, one can obtain a good indication of the *total number of deaths* in that month. Although, on a yearly basis, such a calculation seems fairly robust, this may not hold for months within the year; there could be seasonal variations in the reporting rates. I cannot find a way of testing whether or not this is the case, but as will be seen later (Fig. 1) more deaths are reported in the winter than in the summer. Since

one would have expected there to be more people about in the summer than in the winter, it does not look as if the observed seasonal pattern can be derived from observer pressure alone. Some further possible biases are considered in the discussion. I also examined the proportion of ringed birds that were later reported dead in different regions of the country (see later). I subdivided the country into ten regions (Table 2a). These divisions were partly subjective in that they were designed so as not to divide some of the main studies between different regions. In addition, the data for the breeding colony of birds at Abbotsbury were separated from the rest of the southern counties and treated as a separate unit; earlier studies (e.g. Perrins & Ogilvie 1981) have indicated that the birds there have a rather different life-cycle from those elsewhere.

Table 2a. Regional Divisions of Britain.

1. Southern Counties: Scillies, Channel Isles, Cornwall, Wiltshire, Somerset, Devon, Dorset (except Abbotsbury, see 10 below) Isle of Wight, Hampshire, Sussex and Kent.
2. Thames Basin: Oxfordshire, Berkshire, Buckinghamshire, Surrey and Greater London.
3. Eastern England: Bedfordshire, Cambridgeshire, Huntingdonshire, Essex, Suffolk, Norfolk, Lincolnshire, Leicestershire, Rutland.
4. Midlands: Derbyshire, Gloucestershire, Northamptonshire, Nottinghamshire, Warwickshire, Staffordshire, West Midlands, Herefordshire.
5. Wales: All of Wales and Salop.
6. Northern England: All England north of regions 3 & 4.
7. Scotland: All of Scotland except Hebrides
8. Hebrides
9. Ireland
10. Abbotsbury

For only seven of these regions were there sufficient birds ringed prior to 1975 to give an estimate of the proportion that had been found dead. The data are shown in Table 2b.

Table 2b. The percentage of Mute Swans, ringed prior to 1975, reported dead in different regions.

Region	No. ringed	No. rec'd	%	100/%
Southern Counties	6,625	1,621	24.5	4.08
Thames Basin	5,003	1,376	27.5	3.64
Eastern England	5,377	1,349	25.1	3.98
Midlands	5,896	1,758	29.8	3.36
Wales	371	77	20.8	4.81
Northern England	1,982	530	26.7	3.75
Scotland	920	245	26.6	3.76
Hebrides	1	0	—	—
Ireland	140	17	12.1	8.26
Abbotsbury	153	61	39.9	2.51

Somewhat surprisingly, regional variations

in the reporting rate are not great; for all the areas where large numbers of swans were ringed prior to 1975 the reporting rate is surprisingly similar, varying between 24.5% and 29.8%. Based on small samples, reporting rate was low in Ireland and very high at Abbotsbury. The latter is not at all surprising in view of the fact that many birds live most of their lives on the Fleet at Abbotsbury and that the area is well-patrolled by ornithologists.

Unfortunately, and as already mentioned, the cygnets of any single cohort are not all ringed in

1) The estimated number of deaths in each month is the number of reported deaths in that month multiplied by 3.77.

2) The "pool" of birds alive in any month is the total number ringed prior to that month (less the total number of deaths prior to that month) plus half the number of swans ringed in that month.

3) The monthly death-rate is the estimated number of deaths during that month as a percentage of the pool of birds alive during that month.

Table 3. Method of estimating "pool" of Mute Swans alive.

Month	July	August	September
1) No. ringed in month	100	200	400
2) No. reported dead	5	10	20
3) Row 2 x 3.77	18.85	37.7	75.4
4) Row 1 x 0.5	50	100	200
5) No. survivors at end of month	81.15	162.3	324.6
6) Cumulative "pool" alive during month	50	181.15	443.45
7) Monthly Mortality	37.7	20.8	17.0

Note—

Row 5 = Row 1 - Row 3; Row 6 = Sum of Row 5 for previous months + Row 4; Row 7 = (Row 3/Row 6) x 100. See text for further explanation.

a single month, but each cohort is ringed over a period of rather more than a year. Hence, during that time, the "pool" of birds from which the deaths occur increases as a result of new birds being ringed and decreases as a result of birds dying. The pool for any month was derived as shown in Table 3; the number ringed in each month, less the number estimated to have died during the month (the actual number of birds reported dead multiplied by 3.77) was added to the total carried forward from the preceding months.

One further adjustment was made. Since the birds that are ringed in any month are not all ringed on the first day of the month, they cannot be considered as being at risk for the whole of that month. On the assumption that, on average, birds were ringed equally throughout each month, birds ringed in a month have been treated as if they were at risk for only half that month. Hence, in Table 3 for July, only 50 of the 100 birds ringed in that month are counted as being available to be reported. The following month, the whole of the 100 (less the estimated deaths), plus half the 200 ringed in August are available to be reported and so on; in each month half the number ringed in that month is added to the cumulative number ringed in the previous months and the other half is added the following month.

Hence I used the following:

Results.

1) Overall pattern of survival

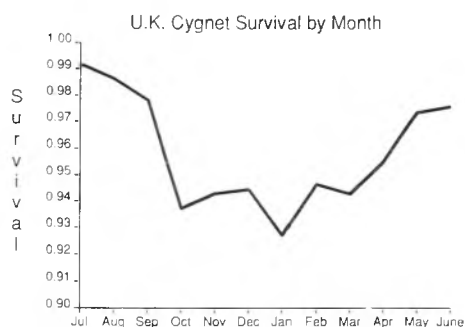


Figure 1. Survival rates per month for young Mute Swans during their first year of life.

The monthly death-rates are converted into survival rates and these are shown in Figure 1 for the first year only. There is a marked annual pattern which is much as would be expected. During the period July to September most young birds remain with their parents; only a few take to the wing before the end of September. During this time they survive well (Birkhead & Perrins 1985). Once they start to fly, their survival rate decreases, in part because they are having to learn to fend for themselves

but also because, in so doing, they are obliged to search out suitable feeding areas and flight is dangerous. Many die as a result of collisions with objects, especially overhead wires (Perrins & Sears 1991).

Monthly death-rates remain high throughout the winter and seem to be especially high in January. This may be related to cold weather (see below). Although Mute Swans are fairly resistant to cold *per se*, they can starve in prolonged cold periods. More important for many birds may be the fact that prolonged cold periods may cause the water they are living on to freeze over and so force them to move, again putting them at risk from flying accidents. From April onwards, the monthly survival rate improves again and mortality is lowest in the middle of the summer, being particularly low in July and August.

The low mortality during the summer months may be, in part, associated with good feeding at that time of year. It is probably also associated with the birds flying less at this time, so not being prone to the hazards that arise from doing so. During late summer every swan is flightless for a period of about six weeks while undergoing its annual moult.

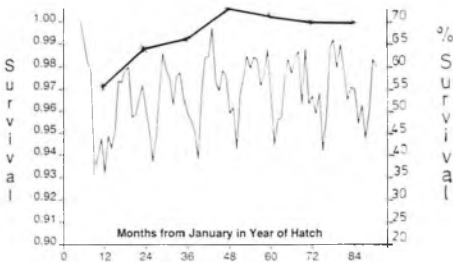


Figure 2. The survival rates, by month, for birds ringed as cygnets, over the first seven years of life. The annual pattern of higher winter and lower summer mortality shows a significant auto-correlation across years ($P < 0.02$) and the increase in survival rate from the first to the fourth year of life is significant ($P < 0.001$) while the change in survival from the fourth to the seventh year is not significant.

Fig. 2 shows a similar analysis, but continued for the first seven years of life. (In most areas of Britain Mute Swans usually start breeding at the age of about three or four). Superimposed on these data are the annual survival rates calculated from them. Two things are apparent from this figure. First, the seasonal pattern of mortality in the first year continues throughout life. Second, there is a slight, but statistically significant, improvement in survival during the first four years of life.

2) Survival in different time periods

Survival in successive five-years periods is shown in Table 4. The differences are not great, though annual survival rates were significantly lower in the periods 1965-69 and 1980-84 than in the other three periods. The first of these two periods is associated, but not exclusively, with the major decline in numbers, especially of the large non-breeding flocks in southern England (Birkhead & Perrins 1986); the survival for the

Table 4. Mute Swan cygnet survival during the first year of life in different periods of time.

Time Period	N	Survival (%)
1960-64	3713	61.3
1965-69	3479	53.6
1970-74	3182	65.3
1975-79	3207	61.5
1980-84	4285	58.0

first five months (July-November inclusive) was markedly lower in this period, than any of the others, being the lowest in four of the five months. The period 1980-84 included the hard winter of 1981.

3) Survival and winter temperatures

To examine the effect of winter weather on survival, the data were sub-divided further into their separate cohorts. This had the disadvantage that the number of birds ringed in several of the years was rather small but made it possible to examine whether there was any relationship between the monthly survival rates in winter and the severity of the weather. The measure of weather used was the screen temperature recorded for Oxford by the School of Geography. Although this cannot be representative of the whole of the country, Oxford is geographically central, especially when considering the distribution of swan ringing in Britain, most being done in the south and the Midlands. Two measures were used. One was the number of days in each month when the minimum temperature fell below zero (number of frost days) and the other was the sum of the degrees below freezing to which the temperature fell (sum of degrees of cold). For example, a day with a minimum temperature of -5°C would contribute one to the first measure and five to the second.

The survival estimates for the five months November, December, January, February and March were compared with the weather measures for the same months. There was a significant tendency for the birds to have lower survival in colder winters.

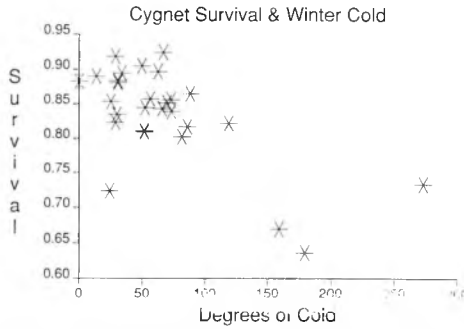


Figure 3. The survival rate of cygnets during the months January to March in relation to the coldness of the winter, as measured by the number of degrees of cold during the months November to January (see text for further explanation). The regression is highly significant ($P < .001$) and has an r^2 of 40.8%.

The level of statistical significance varied with the periods used, but the highest correlations were found with a) a time lag of one or two months between the temperature and the survival rates and b) sums of degrees of cold rather than number of frost days (Fig. 3). A lag between low temperature and high mortality is likely as the birds presumably take some weeks to lose condition as a result of cold weather. There is also the possibility that many birds are not reported until some time after death.

4) Regional Variation

A similar technique has been used to examine the seasonal pattern of deaths in the different regions of Britain (divided as shown in Table 2a). Separate area-specific correction factors (as shown in Table 2b) were used to generate the results for each area.

Using these figures we can calculate, for each area, the survival pattern of juveniles. Except for the population at Abbotsbury, all these areas show seasonal patterns similar to that in Fig. 1, with low mortality in the first few months, higher mortality in winter and lower again the following summer. The correlations between

the different areas are shown in Table 5. It is not surprising that the Abbotsbury pattern is somewhat different. The large majority of the cygnets there are raised in pens; they are ringed and released in September. There are therefore no data for the first two months, July and August, and there is often a small mortality of birds shortly after release.

Hence the overall pattern of mortality is similar in most areas of Britain. Table 6 shows the estimated total survival rate for the first year in

Table 6. Mute Swan cygnet survival during the first year of life in different areas of Britain.

Area	N	Survival (%)
Southern Counties	3261	61.6
Thames Basin	4289	60.3
Eastern England	2579	57.3
Midlands	4501	69.1
Northern England	894	56.7
Scotland	726	55.7
Abbotsbury	941	61.7*

Note: no Abbotsbury data for birds ringed July & August, so estimate is for 10 months only.

each of the main regions. These show that the survival rate only varies from 56% to 62% except for the Midlands where the rate is 69%. The latter area is the one with the poorest nesting success, largely due to vandalism in the urban habitats (Coleman & Minton 1980). The slightly elevated survival rate of the reduced number of cygnets suggests that either there is some form of compensatory survival of the remaining cygnets or that only cygnets from good habitats remain after the heavy nest losses and that their survival is consequently slightly higher than that of cygnets from a wider range of habitat qualities elsewhere.

Discussion.

There are a number of possible sources of error in analyses such as those presented here.

Table 5. Correlation between patterns in different areas.

	Southern Counties	Thames Basin	Eastern England	Midlands	Northern England	Scotland
Thames Basin	0.73					
Eastern England	0.69	0.58				
Midlands	0.86	0.88	0.69			
Northern England	0.79	0.70	0.84	0.74		
Scotland	0.61	0.77	0.64	0.60	0.70	
Abbotsbury	0.76	0.11	0.49	0.38	0.47	0.12

Note— $r > 0.553 = P < 0.05$;
 $r > 0.684 = P < 0.01$

Anderson *et al.* (1985) list a number of assumptions (loc. cit. p.90) that should be met, not all of which are met here. Further, the reliability of multiplying the number of known deaths by a constant can be questioned. It may be wrong for a number of reasons: the reporting rate may have varied with time, with area, may not be constant within years or may vary with cause of death. These points are discussed in order.

1) *Variation with time.* The reporting rate for dead swans seems to have not varied much over the course of the last 25 years.

2) *Variation with area.* Surprisingly, the reporting rate in different areas of the country seems to be fairly constant; one might have expected the reporting rate to vary markedly in response to large variations in human population densities in different parts of the country. Reflection suggests that the relatively constant rate should not be that surprising. Although there are many parts of, say, Scotland where there are few people to report dead swans, in practice swans live on lowland lochs and slow-flowing rivers where there are usually high densities of people. Hence the chance of a dead swan being reported may not be as variable as it would be if it were simply based on human population density measured throughout the whole of each area.

3) *Variation within the year.* The assumption has been made that reporting rates are constant throughout the year. This is untestable and might well not be true. If not, it would affect the calculations. The reporting rate is likely to be affected by the number of people in the countryside (though note that recovery rates are lowest in the summer months, not highest as would be the case if variations in the number of people about was the sole cause of the seasonal variation). The absence of anglers during the closed season for coarse fishing (mid-March to mid-June) could further affect the chances of reporting though this is complicated by the fact that certain deaths, especially lead poisoning (Birkhead & Perrins 1985, Sears 1988) are associated with the presence of anglers. Further, it is possible that the probability of being reported is related to size and colour. Most Mute Swan cygnets ringed in July are not fully grown, though by late August the difference in size between cygnets and adults is usually not great; more important perhaps, these cygnets are brown, becoming progressively whiter throughout their first year. One might expect to find that they were under-recorded, and hence the death-rate under-estimated, while they were in this brown plumage compared with the white

plumage of later life. The results presented here do indeed show very low losses (i.e. very few reported deaths) during July and August. The number of reported deaths rises sharply in September, probably because cygnets start to fly then and may leave their natal territory; many of the deaths come from young birds flying into overhead wires (Perrins & Sears 1991). Nevertheless, observations on broods at this time also show very high survival, so that the high survival shown in Fig. 1 may well be true.

Another problem is that the monthly recovery totals are not strictly independent: a bird reported dead, especially early in a month, might have died in the previous month. Birds that are badly decomposed are usually reported as such, so this is not likely to be a problem, but the patterns such as those in Fig. 1, could be somewhat biased to the right, i.e. some deaths should have been ascribed to the previous month.

4) *Variation in relation to cause of death.* A further possible source of error is the assumption that reporting rate is constant for all causes of death. For example Perrins & Sears (1991) argue that a high proportion of the swans that die from collision with overhead wires are reported. Such birds often disrupt power supplies or telephone lines; the engineers who go out to repair the line are likely to find - and report - the bird. Birds that die from other causes are much less likely to be recorded. If the tendency to hit wires varied very much with area or time, this would further affect the reliability of using a simple correction factor. About 22% of all reported deaths are reported as having died in this way. If all such deaths were reported and all unreported deaths were from other causes, the correction factor for these would have to be 4.55, not 3.77. Fig. 4 shows the data from Fig. 1 replotted in this way; the results are very simi-

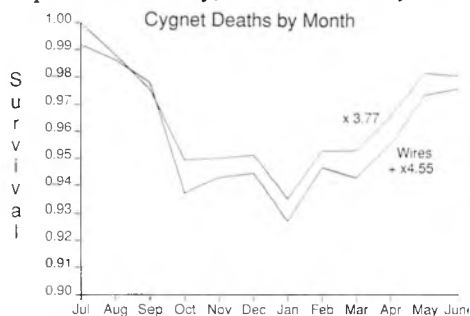


Figure 4. The data from Fig. 1 re-calculated after separating two forms of death. Those birds that were reported as having been killed by wires were not multiplied by any correction factor and were added to the number of birds which died from all other causes of death multiplied by 4.55. See text for explanation

lar, suggesting that this source of error is not important.

A final problem to be considered is the robustness of the use of the correction factor of 3.77. This is based on the assumption (from Table 1) that only 26.5% of swans that die are reported to the Ringing Office. Since the tech-

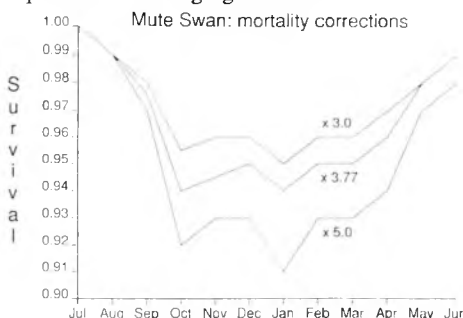


Figure 5. The effect of two hypothetical correction factors (3.0 and 5.0) on the pattern shown in Fig. 1. See text for explanation.

nique used here results in this correction factor affecting both the estimated number of deaths and the number of birds alive from which the deaths can occur, the calculations are heavily dependent on the accuracy of this figure. One can argue from the data that this is the correct figure, but it is necessary to ask what would be the result of using a different correction factor. Fig. 5 gives some indication of this. The same data as in Fig. 1 are plotted against two hypothetical correction factors, 3.0 and 5.0. These results suggest that the technique is fairly reliable for showing the *relative* pattern of mortality in different months, but much less reliable for measuring overall survival.

Notwithstanding these possible sources of error, the observed pattern of mortality is in accord with what might be expected. It is known that the survival of cygnets during August and September, while they remain with their parents, is high (Birkhead & Perrins 1985). Mortality increases once the young birds start to leave their parents' territories in late September, October

and November. These analyses confirm this; the October-November death-rate is statistically significantly elevated over those in the previous months. Thereafter however, the monthly death-rate varies rather little throughout the winter.

Spring is also known to be a period of increased aerial activity with an associated increase in the number of deaths from collisions (Perrins & Reynolds 1967). Recent analyses of deaths from flying into overhead wires (Perrins & Sears 1991), but based on much larger samples, confirm the earlier findings (of Perrins & Reynolds) that first year birds have elevated losses in autumn, though show that those in spring mainly occur in older age groups.

However, overall, the data analysed here do not show peaks in mortality in spring and autumn; mortality rises in October and stays high through April. These calculations are for all losses, not just those from flying accidents. As losses due to flying decrease, losses due to winter mortality (such as those caused by hard weather or food shortage) increase.

Logically, the technique used here for calculating the survival rates of Mute Swans should work for other species, even those with much lower reporting rates. However, it is dependent on a number of features which few birds satisfy. Most important, they probably need to be resident, since marked changes in distribution might be associated with large differences in reporting rates. They also need to be equally likely to be found, when dead, at all times of year. Although, as discussed, this may not be wholly true for the Mute Swan, it is even less likely to be true for, say, small passerines whose probabilities of being found are dependent on the amount of vegetation in gardens or in woods. The high degree of residency, the association with watersides together with the large size and conspicuous whiteness of Mute Swans makes them particularly likely to be seen and hence reported. Indeed, perhaps the surprise should be, not be that 27% of dead swans are reported but, rather, that 73% go un-noticed!

My thanks go to the British Trust for Ornithology and the Swan Study Group for permission to computerise the swan ringing data and the recovery data. Gladys Rance & Agnes Kriksfalvi extracted the data from the ringing schedules. Dr. R.H. McCleery helped greatly with the handling of the computer records and P. Chivers did a lot of sorting of an earlier set of the data. The Oxford University School of Geography kindly supplied the measures of winter weather used for comparing with the winter mortality. I am grateful to Dr R.H. McCleery, Dr. J.D. Lebreton and Dr J. Sears for making useful comments on the manuscript.

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