Variation in the production of young of swans wintering in Sweden

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Studies of swans and geese have revealed marked annual variations in the proportion of young in wintering flocks (e.g. Boyd 1959; Cadbury 1975; Lynch & Singleton 1964; Nilsson 1968; Nisbet 1959; Ogilvie 1969; Owen & Norderhaug 1977). According to Lack (1967, 1968) clutch-size in waterfowl evolved in relation to the amount of food available for the female prior to laying. He also suggests that it would be advantageous for a female to postpone breeding until it can lay the full clutch rather than laying a smaller clutch. Nevertheless, Bengtsson (1971) found a significantly lower clutch for ducks in a year with bad food supply at Lake Mayvatn, Iceland. The importance of winter and spring feeding conditions for the breeding success in waterfowl has been stressed by several workers (e.g. McInnes *et al.* 1974; Ryder 1970).

Data on the proportion of first-winter birds among swans in south Sweden were collected regularly in connection with the International Waterfowl Counts in November and January (Nilsson 1975, 1977). On average about 25% of the Mute Swans *Cygnus olor* and 30–50% of the Whooper Swans *C. cygnus* in the country were so examined.

Results

The proportion of young (first-winter birds) in both species of swans showed marked annual variation (Table 1), and were generally lower in Whooper Swans than in Mute Swans.

Comparing the percentage of young among Whooper Swans in January with temperatures (the means of 4 monthly means) at ten meteorological stations in south Sweden in the *preceding* winter a significant correlation was found (Figure 1). The strongest correlation (r = 0·76) was obtained when the percentage of young was compared with the mean temperatures of the whole period, December–March, but correlations were almost equally strong when the comparison was with the means for the separate months of December, January and February or with these months in pairs (Table 2). Comparison with the mean temperatures in March yielded insignificant correlation. The weather in the winter proper is thus more important than that in early spring.

A local series of counts from Scania, the southernmost province of Sweden, for 1965 to 1976, yielded similar results. The series is included in the national series from 1967 onwards. An earlier series from one important inland locality in south Sweden, Trollhättan by the river Göta älv (Nilsson 1968), did not yield a significant correlation between winter temperatures and the proportion of young in the following year (Table 3). However, if 1961/62, which had a very low percentage of young even after a very mild winter and early spring in Sweden, is excluded, a highly significant correlation results. In 1961/62 the swans arrived much

Table 1. The percentage of first-winter birds among wintering swans in south Sweden 1967–1978. Size of sample in brackets.

Year	Mute *Cygnus olor*		Whooper *Cygnus cygnus*	
	November	January	November	January
1966–67	—	18·2(2645)	—	9·4(820)
1967–68	—	18·2(791)	—	18·6(754)
1968–69	—	22·6(3172)	—	13·6(1606)
1969–70	17·7(2888)	12·3(2749)	3·3(1090)	7·9(1075)
1970–71	17·4(943)	13·5(609)	10·8(343)	7·9(227)
1971–72	35·6(1852)	32·8(1402)	13·9(245)	16·3(1007)
1972–73	38·2(1792)	24·9(1966)	8·7(369)	9·3(690)
1973–74	25·6(2738)	22·8(1185)	24·5(739)	19·6(734)
1974–75	—	16·7(1654)	—	14·6(624)
1975–76	—	20·6(4996)	—	23·7(556)
1976–77	—	8·5(1548)	—	16·4(714)
1977–78	—	—	—	7·0(617)

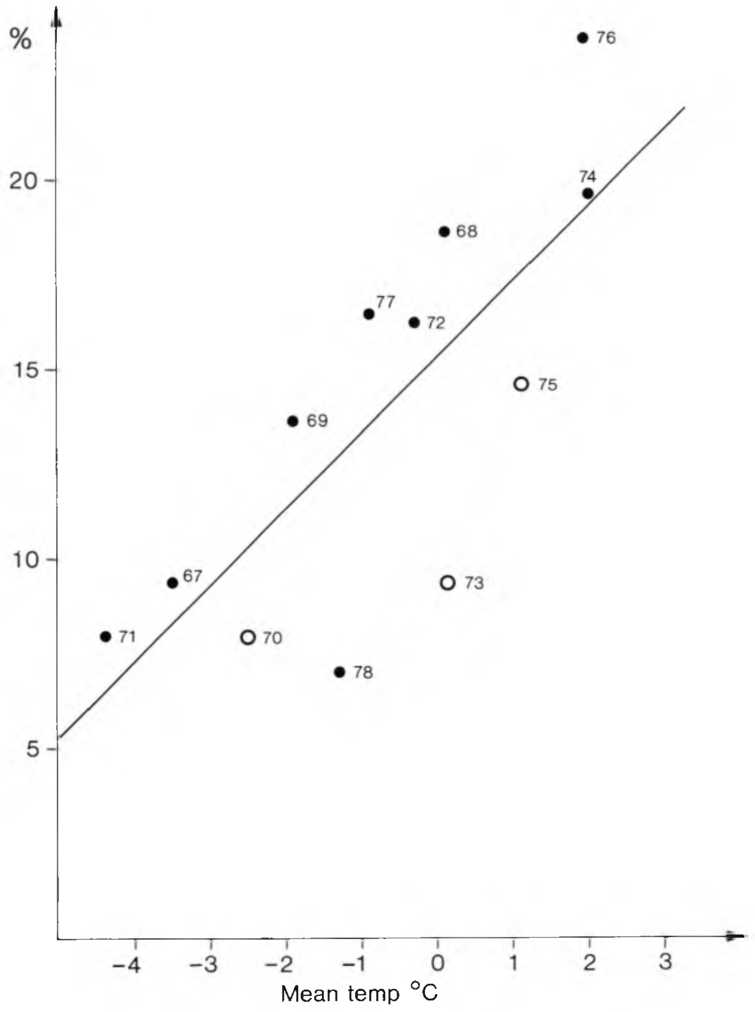

Figure 1. Percentage of first-winter birds among Whooper Swans in south Sweden in January 1967–1978 in relation to mean temperatures for the preceding December–March at ten meteorological stations in south Sweden. Correlation coefficient $r = 0{\cdot}76$ ($P < 0{\cdot}01$), regression coefficient $b = 2{\cdot}05$. Open circles denote winters after a cold spring in the Soviet breeding areas.

Table 2. Correlation and regression coefficients over 12 winters for the relation between the percentage of first-winter birds among Whooper Swans in January and the mean temperatures on the wintering grounds in the preceding winter.

Mean temperatures in preceding winter used	Correlation coefficient	P	Regression coefficient
December	0·660	< 0·05	1·49
January	0·625	< 0·05	1·28
February	0·700	< 0·02	1·28
March	0·423	< 0·2	1·13
December + January	0·720	< 0·01	1·74
January + February	0·716	< 0·01	1·48
February + March	0·676	< 0·02	1·69
December – March	0·761	< 0·01	2·05

Table 3. The percentage of first-winter birds among Whooper Swans at Trollhättan, Göta älv, in 1960/61 to 1967/68 in relation to mean temperatures in the preceding winter and to mean temperatures in the preceding May in the Soviet breeding grounds. [1] = $P < 0.01$, [2] = $P < 0.05$.

Season	First-winter birds %	Mean temperatures (December–March) South Sweden	Local	Breeding grounds May
1960/61	23·6	−1·4	−2·2	7·2
1961/62	6·5	1·6	−1·1	4·4
1962/63	4·2	−1·3	−1·7	8·4
1963/64	4·4	−4·8	−5·4	9·1
1964/65	10·5	−1·6	−1·5	5·5
1965/66	18·9	−0·8	−0·6	2·3
1966/67	9·1	−3·5	−4·6	5·3
1967/68	25·4	0·1	0·0	5·4
Correlation coefficient		0·37	0·38	−0·13
(excl. 1961/62)		0·88[1]	0·79[2]	

later than normal in the study area.

November and January values of the percentage of young were generally similar (Table 1). However, in 1969/70 the percentage of young was markedly lower in November than in January. May 1969 was unusually cold in the Soviet part of the breeding range (mean temperatures for five stations 0·4° compared to normal values of 4–5°) and this may have delayed breeding with resulting late arrival of families in the Swedish winter areas. A similar situation may have obtained in 1961.

The percentage of young among Whooper Swans wintering in south Sweden in 1967–1975 was compared with mean temperatures for five stations in the Soviet breeding area during the previous May (Figure 2). If 1967 and 1971 are excluded from the calculations a highly significant correlation was found. The preceding winters, 1966 and 1970, were the only really cold winters in south Sweden during this period and the low production of young might thus be related to the winter conditions rather than those in the breeding grounds. Similarly the percentage of young in south Sweden in January 1970 and 1973 were lower than could be expected from the winter situation, but cold May weather in the Soviet breeding grounds could explain the low production. January 1978 also yielded lower than expected percentage of young in south Sweden but no data on May temperatures for 1977 (nor for 1975 and 1976) could be obtained.

The data from Trollhättan did not show any correlations with temperatures on the Soviet breeding grounds (Table 3). However, the low percentage of first-winter birds in 1961/62 coincided with fairly low temperatures in the breeding grounds the preceding spring.

In order to try to separate the influences on the production of young, of temperatures on the breeding grounds and those on the winter grounds, the data were grouped according to whether temperatures were above or below average (for the series) for the Soviet breeding grounds and for Swedish winter grounds, respectively. For the five years with above average (= 3·7°) spring temperatures in the Soviet breeding grounds the mean percentage of young was 13.8%, whereas the mean for the four years with colder springs was 12·0%. The mean percentage of young in six years following milder winters than average (− 0·8°) was 17·0%, whereas following the six colder winters it was 10·4%. Only in the latter case was the difference significant ($P < 0.05$, analysis of variance).

In the Mute Swan no significant correlations could be found when comparing winter temperatures in south Sweden with the percentage of young present in the following winter. The correlation coefficient for the comparison with the December to March mean temperature was only 0·23. A somewhat higher but still insignificant correlation was found with March temperatures ($r = 0.42$). Comparisons with spring temperatures for the breeding areas gave similar inconclusive results.

No comparable data on the proportion of young birds in the Whooper Swan elsewhere have been published except for a few years (Boyd & Eltringham 1963; Hewson 1964).

Published information about the proportion of young among Bewick's Swans *C. columbianus bewickii* in Britain (Ogilvie 1969; Cadbury 1975) gave no significant

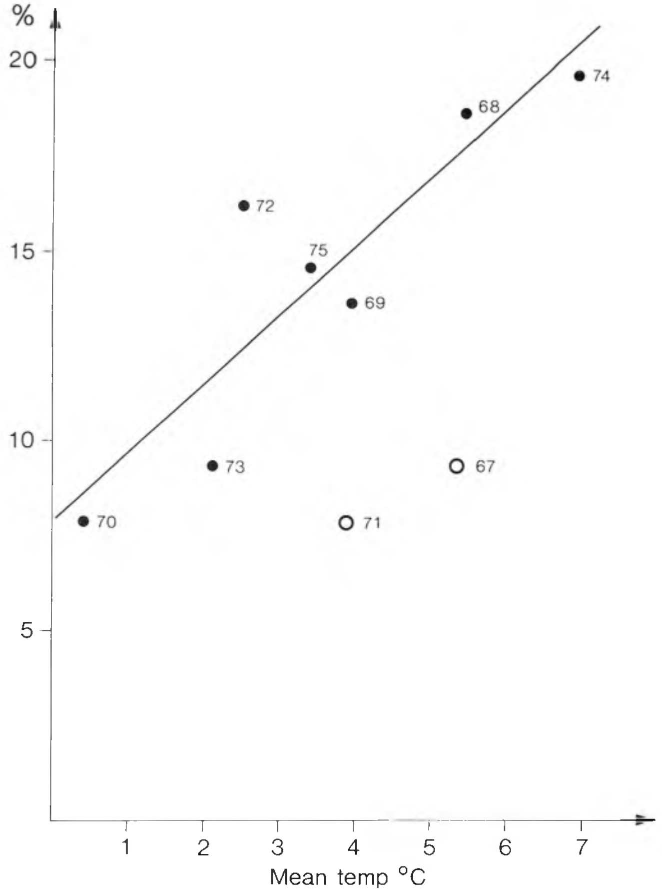

Figure 2. Percentage of first-winter birds among Whooper Swans in south Sweden in January 1967–1975 in relation to the preceding mean May temperatures at five meteorological stations in the Soviet breeding areas. Open circles denote years following after especially cold winters in southern Scandinavia. Correlation coefficient $r = 0{\cdot}57$ ($P < 0{\cdot}1$) for all years, correlation coefficient $r = 0{\cdot}89$ ($P < 0{\cdot}01$) for all years except two years with especially cold winters (1966, 1970, production recorded in January 1967, 1971). The regression line in the graph ($b = 1{\cdot}81$) applies to this correlation.

correlations with winter or spring temperatures (Table 4). However, temperature data were only available from three stations in the breeding areas of the Bewick Swans.

Discussion

It is clear that the production of young in the Whooper Swan is markedly affected by the weather situation in the preceding winter and not only by the situation in early spring, as had been suggested by Lensink (1972) for Whistling Swans *Cygnus columbianus columbianus*.

Sweden is situated in the northern part of the winter range of the species (Nilsson 1975) so low temperatures will freeze important feeding areas. This will affect the availability of food and hence the condition of the females. Indeed in southern Sweden Whooper Swans regularly feed in cold weather on crop lands.

In at least the northern parts of the breeding range Whooper Swans must start breeding on their arrival if the young are to be on the wing before the autumn freeze-up. A late spring will result in too short a period for successful breeding (Haapanen *et al.* 1973). Certainly the birds cannot delay breeding and so attain a better condition. Females which lay in poor condition are likely to have lower production or a complete breeding failure. Thus the feeding situation in

Table 4. The percentage of first-winter birds among Bewick's Swans in England 1960/61–1974/75 (after Ogilvie 1969, Cadbury 1975) **in relation to mean temperatures for England in the preceding winter (November–February) and to mean temperatures in the Soviet breeding areas in the preceding May.**

Season	First-winter birds %	Mean temperatures Winter	Spring
1960/61	30·6	—	−3·6
1961/62	8·9	—	−2·2
1962/63	18·2	2·7	−0·5
1963/64	—	—	—
1964/65	19·9	2·9	−5·1
1965/66	19·5	2·6	−4·2
1966/67	24·4	2·9	−0·9
1967/68	8·3	3·2	−2·0
1968/69	8·0	2·2	−2·1
1969/70	6·7	2·5	−3·0
1970/71	18·5	1·9	−7·1
1971/72	10·5	3·2	−4·1
1972/73	16·0	3·7	−5·7
1973/74	23·3	3·0	−3·6
1974/75	18·8	3·2	−5·1
Correlation coefficients		0·09	−0·17

the winter and nesting areas will have been of crucial importance.

In the more southerly part of their breeding range Whooper Swans are not forced to start breeding immediately after arrival and so can better compensate for inferior winter feeding. However, they are only a part of the population and the overall production will be lower after a late spring. For Bewick's Swans wintering in Britain, winter conditions will probably only rarely be so hard as to affect the future breeding results, especially when given supplementary food as at Slimbridge and at Welney on the Ouse Washes. In this arctic breeding species the weather on the breeding grounds will probably account for most of the yearly variation in the production of young even though no correlations with spring temperatures there could be found. Local conditions not apparent in monthly mean temperatures, such as sudden snowfalls, will probably be of greater importance. In a study of Svalbard Barnacle Geese *Branta leucopsis*, Owen & Norderhaug (1977) stated that the winter conditions during the years they studied were sufficiently good to put the geese into optimal condition before leaving Britain. Factors in the breeding areas were thus considered to be the main cause of annual fluctuations.

In the Mute Swan, Reynolds (1972) found a clear correlation between weight and subsequent success. However, no correlations between the conditions in the winter quarters and the future production of young were found. Perhaps, so far south it is possible to postpone the start of breeding after a cold winter and late spring to enable the female to attain a good condition before starting to lay.

When viewing these differences in three species of swans it must be remembered that the present distribution of the Whooper Swan is a result of heavy persecution in earlier years. The boreal Whooper Swan was formerly distributed over a large part of the coniferous zone that covers large parts of Fennoscandia and the Soviet Union. Nowadays it is mainly restricted to the northernmost extremes of the former breeding area. In the southern parts of the former breeding area the ice-free season is longer, and delayed breeding, as in the Mute Swan, would have been possible.

Acknowledgements

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Summary

The percentage of first-winter birds was recorded among Whooper Swans *Cygnus cygnus cygnus* and Mute Swans *Cygnus olor* in south Sweden,

1960–1978. A marked variation was found between different years. In the Whooper Swan a significant correlation was found between the temperature in the winter quarters and the production of young in the following summer, whereas no such correlation was found in the Mute Swan. The production of young in the Whooper Swan was also significantly correlated with May temperatures in the Soviet breeding areas.

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A brood of Mute Swans *Cygnus olor*. (*Philippa Scott*)