Annual variation in the reproductive performance of Goldeneyes

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The sizes of avian clutches and broods and the timing of breeding have been found to vary considerably from year to year (e.g. Lack 1966; Klomp 1970). This variation between breeding seasons has been related to, for example: changes in population density of Great Tits (Krebs 1970); changes in the prevailing weather conditions in different years for a variety of species (Lack 1966); and changes in food supply in Long-tailed Skuas *Stercorarius longicaudus* (Andersson 1976). Among Common Eiders *Somateria mollissima* and the dabbling ducks there is some evidence of variation in clutch sizes between years although this does not, generally, appear to be the case in the diving ducks (Bengtson 1971; Milne 1974, 1976a). It has been demonstrated, however, that in certain ducks (e.g. Mallard *Anas platyrhynchos:* Langford & Driver 1979) the timing of breeding shows marked annual variation and appears to be delayed by inclement spring weather on the breeding grounds. In general, tundra-nesting geese also delay breeding until suitable spring conditions (the time of the snow melt) which may vary in different years by up to three weeks (Newton 1977).

An opportunity to investigate annual variation in clutch sizes and timing of breeding of the Goldeneye *Bucephala clangula* arose from a long-term study of female Goldeneyes breeding in Central Sweden. This paper describes changes between different years in the reproductive performance of females, i.e. (i) the size of clutches they lay; (ii) the number of young they hatch; and (iii) the dates on which they start egglaying and hatch their young. These changes are examined in relation to two factors which may influence the reproductive performance of Goldeneye females in different years: firstly, changes in the prevailing weather conditions and, secondly, fluctuations in the density of the breeding population. Both these factors are discussed in greater detail by Dow (1982). Comparisons are also made with fluctuations in another detailed study of breeding Goldeneyes in south-west Sweden (Eriksson 1979).

Methods

The study was conducted from 1959 to 1980 in an area of 50.5 km^2 in Central Sweden (59°34'N, 14°8'E). This area is described in detail by Dow (1982). Goldeneyes were recorded breeding in nest boxes (n = 101) and natural cavities (n = 6; henceforth included with the nest boxes) located around the waterbodies.

From 1960 onwards visits were made to each nest box in late April or May, and accurate records were kept of the number of nest boxes occupied by Goldeneyes and the number of eggs in each box. Nest boxes with clutches were revisited to determine brood sizes (from 1960 to 1980) and hatching dates (from 1968 onwards). If the young had left the box, the brood size was determined by subtracting the number of unhatched eggs from the original clutch size. Clutches were categorised as (i) successful: one or more young hatched; (ii) unsuccessful: no young hatched. The date on which the first egg of the clutch was laid (egglaying date) was determined by backdating: subtracting from the hatching date the mean incubation period (30 days) and the number of days taken to lay the clutch. The latter was estimated by multiplying the average number of days it took to lay one egg (1.32) by the clutch size.

Measurement of climatic variables

Daily temperature readings (mean, minimum, maximum) in April and the date of the break-up of the ice on the main lakes in the study area were provided by the Swedish Meteorological Office in Norrköping for stations (Filipstad or

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Persberg) within 20 km of the study area. Data for winter temperatures (average mean monthly temperatures in September to April for ten stations in southern Sweden) were provided by Leif Nilsson (University of Lund, Sweden). The term 'winter temperature' represents the average of these mean monthly temperatures from December to March inclusive.

Results

Variation in reproductive performance between years

(i) Sizes of clutches and broods

Although the mean sizes of clutches, including unsuccessful ones, fluctuated in different years, from 7.1 in 1969 to 9.4 in 1961, the variation was not significant (Figure 1). Similarly the size of those clutches which hatched successfully ($\bar{x}$ = 8.7 ± 0.1 eggs) and broods ($\bar{x}$ = 8.1 ± 0.1 young) (which were highly correlated $r = 0.90$; $p < 0.001$; N = 343) fluctuated in different years, but again the variation was not significant. The distribution of clutch and brood sizes did not vary from year to year since there was no significant heterogeneity of variances among years. Furthermore, there was no indication that hatching success (the percentage of eggs which hatched in clutches in which at least one young hatched: $\bar{x}$ = 93.4%) varied among years.

(ii) Timing of breeding

The majority of females commenced egglaying in mid to late April ($\bar{x}$ = 25th April; N = 206), but the dates on which

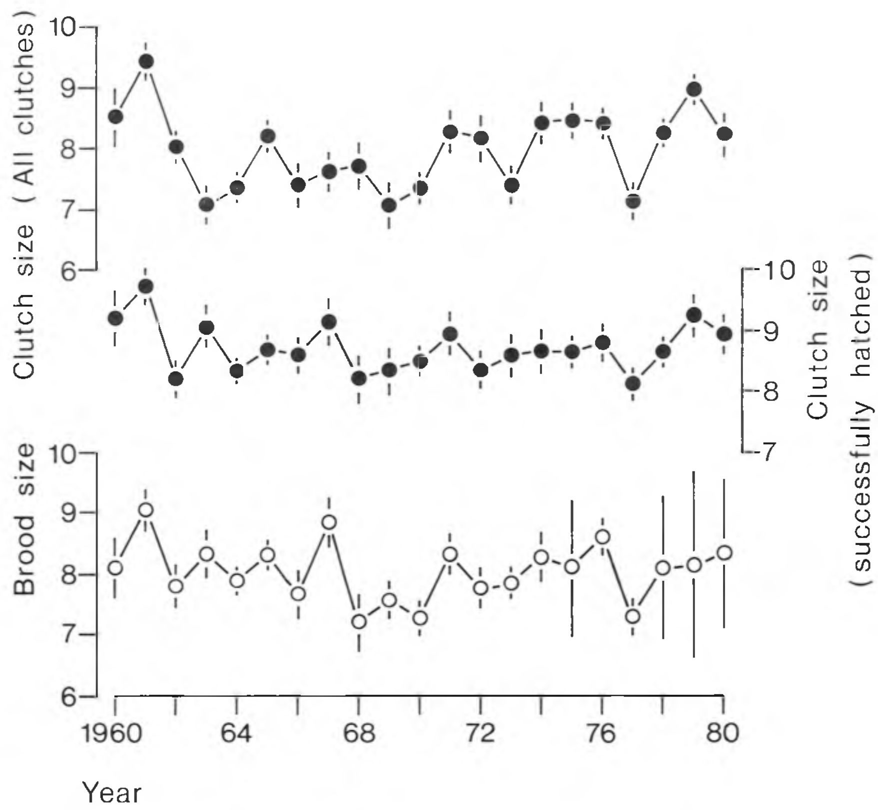

Figure 1. Changes, from year to year, in the size of clutches and broods. The mean (± SE) size of (i) all clutches, both successful and unsuccessful (●–●), (ii) clutches which were hatched successfully (●–●), and (iii) broods (O–O) are given for the period 1960 to 1980 inclusive.

the first eggs of clutches were laid differed significantly between years (Figure 2: Anova: $F = 3.8$; $p < 0.001$; d.f. = 12 & 193). Variation in the timing of egglaying from year to year was considerable; there was a 20-day difference in the mean date between the earliest breeding season (1974) and the latest one (1969). The dates of hatching ($\bar{x}$ = 5th June), being highly correlated with the dates of egglaying, also differed significantly between years. There was no significant variation between years in the spread of the breeding season.

These changes in the dates on which females started egglaying showed similar fluctuations, from year to year, to those recorded in another study area in south-west Sweden (Figure 3).

Factors related to changes in reproductive performance between years

(i) Climatic conditions

Climatic variables were evidently important in determining the timing of breeding. Egglaying started earlier in breeding seasons which followed mild winters than in those which followed cold winters (Figure 4; $r_s = -0.74$; $p < 0.05$; $N = 13$). The mean date of egglaying in any year was significantly negatively correlated with the mean temperatures in the preceding December, January and February (Table 1) but not with those in March.

Egglaying also tended to be earlier in years in which there were high temperatures in April (particularly early April) and in which the ice broke up early on the main lakes in the study area (Table 1). A Step-Wise Multiple Regression Analysis indicated that (a) the mean daily temperatures in the preceding winter and (b) the maximum daily temperatures in early April accounted for much of the annual variation in egglaying dates (Multiple $R = 0.88$; $R^2 = 0.77$; the date of egglaying expressed as the number of days after 1 April = $18.2 - 2.12a - 1.58b$). The spread of the breeding season (as measured by the variance in egglaying dates) was not, however, significantly related to temperatures in either the preceding winter or in the spring.

It does not appear that females delayed the start of egglaying until the immediate onset of favourable temperatures on the breeding grounds, since the mean temperature recorded during the egglaying period (i.e. on days within 95% confidence intervals of the mean egglaying date) varied considerably from 1.82 ± 0.99°C in 1978 to 9.62 ± 0.94°C in

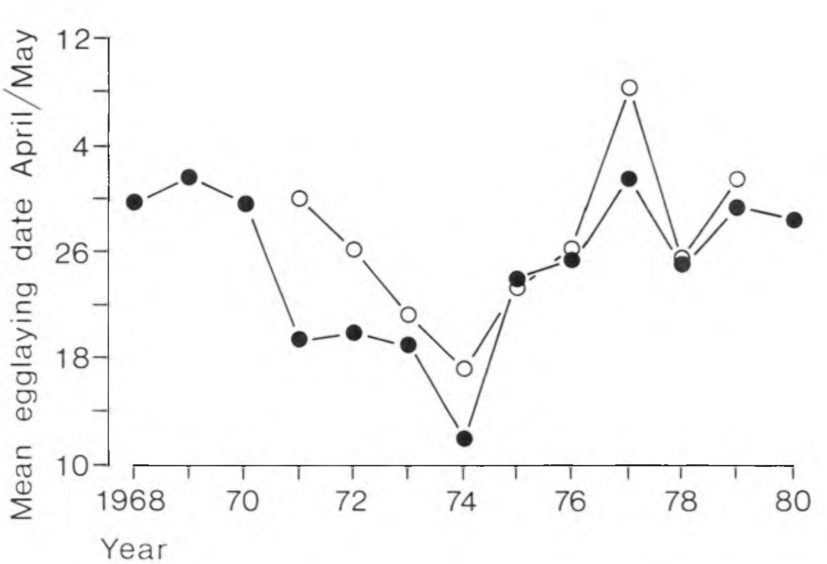

Figure 2. Changes from year to year in the timing of breeding. The mean (± SE) dates of egglaying (●–●) and mean dates of hatching (O–O) are given for the period 1968 to 1980 inclusive.

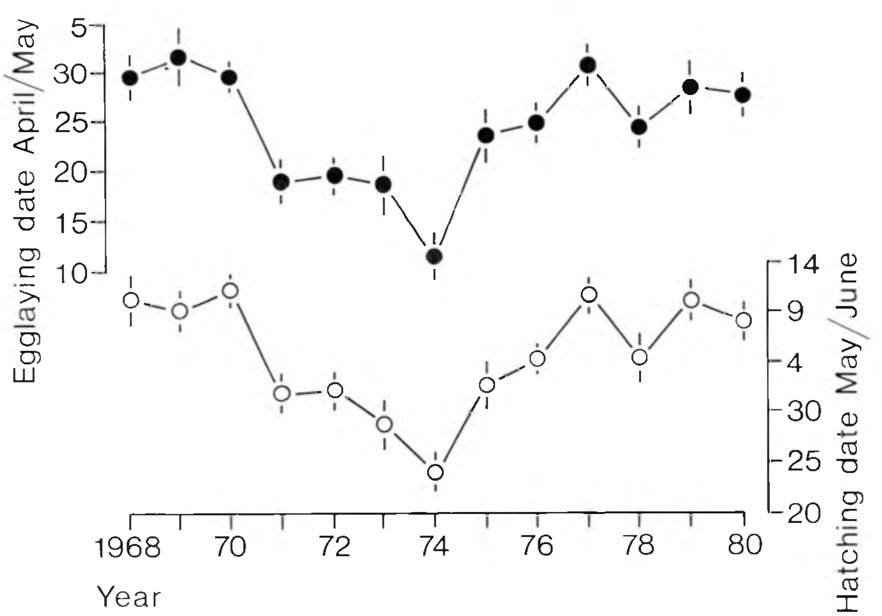

Figure 3. Fluctuations between years in the dates of egglaying in the present study population (●–●) and those in another population of breeding Goldeneyes in southwest Sweden (O–O). Data for the latter are given by Eriksson (1979) and cover the period from 1971 to 1979 inclusive.

Table 1. The correlation between various measures of temperature in the preceding winter and in the spring and the mean dates of egglaying during the period 1969 to 1980 inclusive.

	Climatic variable (temperature °C)	Correlation with the mean date of egglaying
December	mean daily	−0.53 *
January	mean daily	−0.60 *
February	mean daily	−0.79 ***
March	mean daily	−0.45 n.s.
April	mean daily	−0.40 n.s.
April	mean daily minimum	−0.22 n.s.
April	mean daily maximum	−0.40 n.s.
Early April (first 10 days)	mean daily	−0.60 *
Early April (first 10 days)	mean daily minimum	−0.58 *
Early April (first 10 days)	mean daily maximum	−0.48 *
Date of ice break-up	number of days after 1 April	0.51 *

***, ** and * represent significant levels of $P < 0.001$; $P < 0.01$; and $P < 0.05$ respectively.

1968. Similarly the temperature during the ten days prior to the start of the egg-laying period differed widely from 1.14 ± 0.30°C in 1973 to 7.54 ± 0.58°C in 1968.

The sizes of clutches and broods were not, apparently, related to changes in the climatic conditions. There were no significant correlations between temperatures in the preceding winter or those in the spring, and either the means or the variances of clutch and brood sizes.

(ii) Size of the breeding population

The annual number of breeding attempts

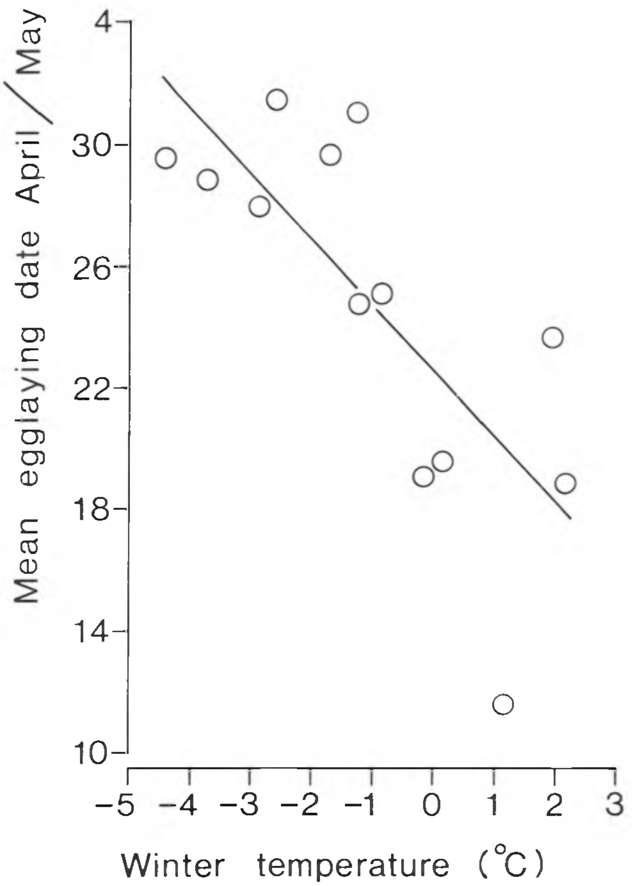

Figure 4. The relationship between the mean date of egglaying and the average temperature (°C) in the preceding winter (December to March). $r_s = -0.74$; $p < 0.05$; $N = 13$; $y = 22.6 - 2.2x$.

by Goldeneyes in the study area fluctuated from a minimum of 22 (in 1959) to a maximum of 44 (in 1976), but did not, overall, vary significantly among years (Fredga & Dow 1983). Clutch sizes and brood sizes do not appear to be density-dependent since the means and the variances of clutches and broods in any year were not significantly correlated with the number of breeding attempts in those years. Nor were the dates of egglaying or hatching related to the size of the breeding population.

Discussion

In common with many other species of diving duck (Milne 1976a) there is no evidence for the Goldeneye of marked variation in clutch or brood sizes between years. This is somewhat surprising since the prevailing weather conditions, the timing of breeding and presumably, therefore, the availability of food and the condition of the females varied considerably. Bengtson (1972) found that the closely related Barrow's Goldeneye *Bucephala islandica*, breeding in Iceland, has smaller clutches in years of high population density. It is worth noting that, in contrast to Common Goldeneye, Barrow's Goldeneye are known to be highly territorial. It is possible, therefore, that the territories of Barrow's Goldeneye are smaller in years of greater population density when access to food may be more difficult. Unfortunately we have no data available with which to estimate the proportion of females which did not attempt to lay a clutch in years with poor weather conditions. However, Fredga & Dow (1983) have found the number of females deserting their clutches was higher in years with a late start to breeding than in years with an earlier start.

It would appear that although Goldeneyes are able to assimilate adequate body reserves to lay similarly sized clutches in different years, the date by which they are able to produce these clutches varies considerably in relation to the temperatures in the winter and the spring. In general, egglaying by Goldeneyes started later following cold winters: since Pehrsson (1975) reports that departure from the migrating areas is delayed under such conditions, it is likely birds arrive later on the breeding grounds in these years and so egglaying starts correspondingly later. This would be in contrast to tundra-nesting geese where the arrival dates are fairly constant from year to year but the date on which breeding commences is delayed until the onset of the snow melt (Newton 1977). The close parallels between the dates of egglaying of Goldeneyes in the present study and of those breeding further south in Sweden suggest that the timing of breeding is related to general changes in climatic conditions on the overwintering or migrating grounds. Possibly Goldeneye breeding further north have more constant arrival dates on the breeding grounds whereas southerly populations respond to the conditions on the migrating grounds to determine their arrival dates (see Pehrsson 1975). Hildén (1964) found a similar relationship between winter temperatures and the timing of breeding of Tufted Duck *Aythya fuligula* in Finland. But like Mallard (e.g. Dane & Pearson 1971; Langford & Driver 1979) egglaying by Goldeneyes was also later when there were cold spring temperatures on the breeding grounds. It would appear, however, in the case of the Goldeneye, that midwinter temperatures have more marked effects than spring temperatures on the timing of breeding.

Bengtson (1971) raised the possibility that there is less food available for females to get into breeding condition in 'late' springs. This may be one explanation for the delay in the onset of breeding in these years, although it is not yet clear when Goldeneyes accumulate the reserves for egglaying and incubation. In tundra-nesting geese (e.g. Newton 1977; Ankney & MacInnes 1978) and early nesting ducks (e.g. Pintails *Anas acuta*, Krapu 1974 and Eiders *Somateria mollissima*, Milne 1976b) the females arrive on the breeding grounds with adequate body reserves to undertake breeding. In contrast, Northern Shovelers *Anas clypeata* spend up to three weeks on the breeding grounds accumulating reserves before starting to breed (Afton 1980).

What might be the reproductive consequences of the annual variation in the timing of breeding for the survival of young? Dow (1982) has shown that survival of young Goldeneye to an age of at least three months appears to be independent of the brood size but lower amongst broods hatched later in the year. Young hatched later have less time available to grow and reach maturity before the onset of winter. There may also be costs to the adults of breeding in 'late' seasons if this, in some way, reduces the likelihood of survival to the next year. Nilsson (1979) reported that reproductive performance (number of young surviving to the winter) of Whooper Swans *Cygnus cygnus* is lower following severe temperatures in the preceding winter. Again low temperatures during the midwinter months (December, January and February) seemed to be of particular importance.

Acknowledgements

We should like to thank Svenska Jägareförbundet, Värmlands läns Jaktvärdsförbund and the British Association for Shooting and Conservation for assistance in the field and financial backing. Hilary Dow was supported by a Science Research Council Studentship. Stewart Evans and Chris Spray kindly commented on earlier drafts of the manuscript.

Summary

Annual variations in the reproductive performance of female Goldeneye *Bucephala clangula* breeding in Sweden is described for the period 1960-1980. No significant differences were detected for clutch or brood sizes between years. The dates on which females started egglaying did, however, vary considerably in different years. The timing of egglaying and hatching was significantly later following colder winters and during colder springs.

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