Factors affecting laying date in the Common Eider

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Introduction

In a paper on the timing of birds' breeding seasons, Perrins (1970) discussed factors affecting date of egg-laying, which included the age of the parents, the length of the pair-bond, the availability of food prior to laying, and the individual ability of birds to obtain food. Milne (1974) considered that the term 'availability of food' for the Common Eider *Somateria mollissima* needed to incorporate the feeding strategy of the pair, and that the role of the male may be as important as the actual amount of food present in the time period immediately prior to laying. If females with weak pair-bonds were given less protection by their mates against the sexual intrusions by other males in the population, then these females may be unable to feed as effectively as those with strong pair-bonds. Milne further postulated that the strength of the pair-bond was influenced by the period for which the pair were together. This implies that later paired females would feed less effectively, and would take longer to attain the minimum pre-breeding weight.

This study assesses the significance of the age, pre-laying weight, and the date of pair-formation of the female, in relation to the date of laying.

Methods

Observations were made on the Common Eider population in the Ythan estuary, Aberdeenshire, Scotland (57°19′N, 2°00′W) during 1973 and 1974. Large numbers of the population have been ringed as fledglings each year since 1961 (Milne 1965, 1974) so that many were birds of known age. To enable identification of individuals a total of 230 females and 115 males were given wing-tags similar to those developed by Anderson (1963), and a further 50 previously tagged females and 15 previously tagged males were identified on the estuary during the study. Tagged birds were identified by means of a 15–60x zoom telescope.

Pre-laying weights were obtained for only a small sample of individuals (n = 22), although weights of a larger number of females were obtained at the time of hatching (n = 71). Since pairing was considered to be a process which occurred over a period it was difficult to allocate a specific date to pair-formation. However, tagged females were regarded as paired when regularly observed keeping close to a male either flying or swimming together, displaying or copulating. Date of laying of individuals was determined both by their absence from the estuary whilst laying and incubating, and by recording the dates when they first reappeared on the water with young ducklings.

Date of laying in relation to age of female

The laying dates of females of different ages are given in Table 1. Significantly more 2 and 3-year-olds laid late rather than early in the season (i.e., laid after the mid-point in laying dates). In these samples all the 2-year-olds and some unknown proportion of the 3-year-olds would be first-time breeders, whereas birds older than three years would almost certainly have bred previously.

Table 1. Date of laying related to age of female. Determined by hatching dates in 1973, and by absence from the estuary in 1974.

Date of onset of laying	1973 number of females aged			1974 number of females aged	
	2	3	3+	2–3	3+
Before 24 April	0	0	4	0	4
24–30 April	0	1	12	1	20
1–7 May	4	4	13	3	19
8–14 May	2	3	7	5	14
15–21 May	2	2	4	4	9
After 21 May	2	1	1	4	4
Totals	10	11	41	17	70

Aged 2 + 3 *v.* 3+, before *v.* after 1 May. $\chi^2 = 9{\cdot}0$, $p < 0{\cdot}01$ (1973), $= 5{\cdot}6$, $p < 0{\cdot}05$ (1974).
Aged 2 + 3 *v.* 3 +, before *v.* after 7 May. $\chi^2 = 4{\cdot}8$, $p < 0{\cdot}05$ (1973), $= 7{\cdot}4$, $p < 0{\cdot}01$, (1974).

Date of laying in relation to body weight of female

There was a tendency for females of above average weight (above $\bar{X}$ + 1S.D.) in March to lay earlier than those of below average weight although the sample size is too small for statistical analysis (Table 2). However, if the spread of laying is divided at the mid-point into 'early' and 'late', then the early breeders were either average or above average in weight, whereas the late breeders were either

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Table 2. Date of laying related to pre-laying weight in 1974.

Date of onset of laying	Pre-laying weight (March 1974)		
	Above average	Average ($\bar{X} \pm$ S.D.)	Below average
Before 1 May	3	1	0
1–7 May	1	5	1
8–14 May	0	5	1
15–21 May	0	2	2
After 21 May	0	0	1
Totals	4	13	5

Table. 3. Date of hatching (1973) related to weight of female at hatching.

Date of hatching	No. of females	Body weight ($\bar{X} \pm$ S.E.)g.
21–25 May	6	1420 ± 62
26–30 May	14	1417 ± 29
31–4 June	21	1413 ± 21
5–9 June	11	1407 ± 42
10–14 June	11	1447 ± 32
15–19 June	7	1394 ± 41
20–24 June	1	1365

$F = 0{\cdot}34$, $p > 0{\cdot}05$.

Table 4. Date of laying (1974) related to date of pairing.

Date of onset of laying	Number of females paired	
	Before 22 Dec.	After 22 Dec.
Before 24 April	1	0
24–30 April	5	0
1–7 May	8	0
8–14 May	9	0
15–21 May	5	2
After 21 May	1	1
Not lay	6	10
Totals	35	13

Table 5. Laying of individual females in consecutive seasons.

Date of onset of laying	Number laying
Both seasons before 7 May	20
1973 before, 1974 after 7 May	4
1973 after, 1974 before 7 May	1
Both Seasons after 7 May	18

$X^2 = 25{\cdot}5$, $p < 0{\cdot}01$

average or below average in weight ($X^2 = 20{\cdot}0$, $p < 0{\cdot}01$).

The date of hatching was not related to the weight of the female at hatching in 1973 (Table 3).

Date of laying in relation to time of pair formation (Tables 1 and 4)

There was no significant difference between the distribution of laying dates of females paired before mid-winter (22nd December) compared to all females in the population ($X^2 = 2{\cdot}2$, $p > 0{\cdot}5$). However, females paired after mid-winter either laid late or not at all. Furthermore, the incidence of non-breeding among these late paired birds (77%) was significantly greater than among early paired birds (17%) ($X^2 = 17{\cdot}6$, $p < 0{\cdot}01$).

Date of laying in consecutive seasons

Laying dates (estimated from hatching dates) of 39 individuals found breeding in two consecutive seasons were significantly related (Table 5). Most females either bred early or late in both seasons. The five changes that occurred were all by females laying near the middle of the season. Milne (1963) also found that some females characteristically bred early in the season, others late.

Discussion

The clutch size of Eiders decreases and predation of nest contents increases as the season progresses (Milne 1974), which would suggest a selective advantage for females laying early in the season. It has been established for several species that females breeding for the first time lay later than older birds (Perrins 1970), and the present study suggests that this is also true for Eiders. Even so, there is considerable variation in date of

laying within each age class. The main cause of such variation may be the different individual ability of females to find food (Perrins 1970), but quantitative evidence to support this is very difficult to collect.

It is not surprising that no differences were found in female weight at hatching through the season; probably, a certain minimum weight must be reached before laying is attempted. Furthermore, early (heavier) breeders may 'lose' more weight as a result of laying more or heavier eggs, and hatching weights refer only to successful breeders; light-weight females may not even complete incubation. More pre-laying weights (taken in March or early April) are needed to verify the relationship between weight and date of laying.

Late (spring) paired females either bred late or not at all. These females were mostly young birds pairing for the first time, although some were older birds possibly forming new pair-bonds. Their feeding is likely to be affected by parties of courting males, which are then most active (McKinney 1961). However, date of pairing was not closely related to laying date of females paired before mid-winter. Thus, early pair formation does not ensure early breeding. Some other factor such as the ability of individuals to find and obtain food must be influencing date of laying.

Our hypothesis is that each female has an individual minimum laying date (and maximum clutch size?) that is genetically determined, either directly or indirectly through a mediating factor such as feeding ability. Thus, it was shown that individual female Eiders tended to have a characteristic laying date, as in several other species (e.g. Kluijver 1951; Richdale 1957; Serventy 1963; Harris 1966; Spurr 1975). However, the potential reproductive capacity of an individual Eider may not be achieved for several seasons, such as interference with the feeding female by other birds (especially males) as the result of a weak pair-bond.

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Summary

Date of laying in Common Eiders *Somateria mollissima* is influenced by several factors. Young (2- and 3-year-old) birds tended to lay late in the season. Females paired after mid-winter (22nd December) also bred late (or not at all), most of these were young birds. Date of laying was apparently not related to date of pairing for females paired before mid-winter. Pre-laying weights (in March) were average or above average for early breeders and average or below average for late breeders. These weights may reflect differences in feeding ability. Individual females bred at a similar time in successive seasons. Each female may have a minimum laying date that is genetically determined, either directly or indirectly, through a mediating factor such as feeding ability.

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