A function of the pairbond in the Common Eider

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The male Common Eider *Somateria mollissima* normally plays no part in the care or protection of nest, eggs, or ducklings. Despite this, the species does not have a promiscuous mating system; the male forms a pair with one female to whom he remains closely attached during the period prior to laying.

On the Ythan Estuary, Aberdeenshire, where the Eider population has been intensively studied, pair formation begins from September onwards (Gorman 1974), although laying is not until the following spring. The female selects and prepares the nest-site, and undertakes the 26-day incubation; during incubation she remains in the nest except when disturbed, and does not normally feed (Gorman & Milne 1972). The male accompanies the female in all activities before and during egg-laying, but remains on the estuary when incubation begins (Milne 1974).

Before laying, the female must obtain enough food additional to that normally required, not only to form the clutch of large eggs but also to lay down sufficient fat reserves for the incubation period (Milne 1974). The female's ability to collect this extra food is likely to be an important factor determining her subsequent breeding success, both in terms of clutch size and in success in hatching the clutch; the main causes of egg loss are desertion and predation, both becoming more probable if the female has to leave the nest to feed during incubation (Milne 1974). Hence anything affecting her feeding efficiency prior to laying may affect her subsequent productivity.

The female must increase her food intake at a time when sexual display and competition for females (intensified by an excess of males in the population) is at a peak (Milne 1974). Why should there be a pairbond at all in Eider ducks since the male takes no part in the care of nest, eggs or young, and why does pair formation take place so early? This study tests the idea suggested by Milne (1974), that interactions with other birds can reduce females' feeding rates through disturbance, and that a function of the pairbond in the prelaying period is for the male to protect the female from any such disturbance.

Method

The hypothesis was tested by measuring firstly the relationship between females' feeding rate and the number of interactions with other birds, and secondly whether the female's mate had any effect on this relationship. Observations were made during May and June 1972, covering the pre-laying and laying period.

(a) Measurement of feeding rate

On the Ythan estuary, most of the Eiders' diet consists of mussels *Mytilus edulis* which are mostly collected by dabbling (Marriott 1966). Previous studies of feeding behaviour (Marriott 1966; Love pers. com.) suggest that a reasonable estimate of feeding rate, as items taken per unit time, can be made by counting the very conspicuous movements of the bill as the bird swallows an item after lifting its head from the water. As Eiders may swallow items underwater, this method gives a minimum feeding rate.

Minimum feeding rates were therefore measured by counting the number of swallows by individual feeding ducks in 3-minute observation periods.

(b) Interactions with other birds

In the aggregations of Eiders feeding on the mussel beds, there were frequent interactions between birds. These were usually either aggressive encounters between pairs or males courting females. Both could have an adverse effect on the females' feeding rate. The most usual female response to either situation was 'chinlifting' alternating with threat displays; when her mate is present this often forms an inciting display, but is also performed when the mate is not present (full details in McKinney 1961). It was not always possible to tell at which other birds the chinlifting and threat displays were directed, and consequently with how many birds the female interacted. Therefore in the three-minute observation period the number of chinlifts and threat displays and also the number of attacks and chases involving her, were recorded.

Since the presence of other birds may depress feeding rate by keeping the female alert, flock density was recorded as follows: dense—the bird is surrounded by others on all sides, and inter-individual spacing is less than 10 eider-lengths; medium—the bird is on the edge of a dense flock or in a flock where inter-individual spacing is more than 10 eider-lengths; isolated—except for mate.

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(c) Role of mate

A male was assumed to be a female's mate if he chased off other birds approaching her, especially in response to inciting, and if he consistently followed her closely and this did not provoke threatening behaviour from her.

A very few paired males defended a small area round their mates against all other eiders, allowing the female to feed uninterrupted. Many males did this some of the time, but most only threatened and chased off other birds which the female was threatening, or in response to her inciting. The number of times the female's mate threatened or chased off other birds was recorded.

The mere presence of the male close to the female may give her some protection against interruption. The mate's position was therefore recorded as: close—the male nearly always within 10 eider-lengths; close/far—the male spending part of the period close to, and part far from the female: far/absent—the male absent or nearly always more than 10 eider-lengths away.

It is possible that some males were wrongly recorded in the far/absent category. Similarly, a few females whose mates were recorded as far/absent may in fact have been unpaired.

(d) Choice of bird for observation

The observations were mainly made on individual females, between 0900 and 1800 hours, through all stages of the tidal cycle when birds were feeding.

Observations were only made on clearly visible feeding birds and were abandoned if the bird went out of sight or stopped feeding. Birds in different flock densities were observed in roughly the same proportions as these occured. Otherwise choice of bird was random.

Results

Effect of behavioural interactions on females' feeding rate.

This was assessed by plotting feeding rate (items per minute) against number of display movements shown by the female (see Figure 1). Observations including attacks or chases involving the female were not included in this plot as the effect on feeding rate is probably not of the same magnitude. The plot shows a significant linear negative relationship between feeding rate and the number of displays ($p = <0{\cdot}001$).

It could be argued that, rather than behavioural interactions lowering feeding rate, females only display during pauses in feeding. However, the fact that females did not appear to initiate these interactions, frequently attempted to feed during them and returned to feeding immediately afterwards suggests that this was not the case, and that interactions with other birds have the effect of lowering the female's feeding rate.

Effect of flock density

Analysis of variance show a significant difference ($P = 0{\cdot}008$) between feeding rates in different categories of flock density due to the higher rate in medium density flocks (Table 1).

Denser flocks presumably form on the better feeding areas, but the effect of this on feeding rates will be masked by the greater number of behavioural interactions as shown

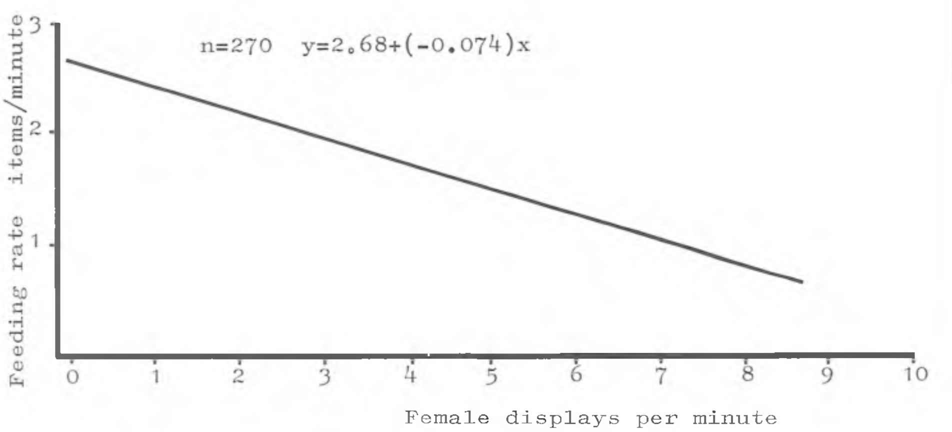

Figure 1. Female feeding rate in relation to number of displays given.

Table 1. Female feeding rate at different flock densities.

Flock density	no.	Mean feeding rate (items/min.)	Mean no. display movements/min.	% observations with female involved in attacks and chases
Dense	87	2·20 (s.d. = 0·93)	2·12	14·9
Medium	111	2·62 (s.d. = 1·03)	0·97	9·0
Isolated	38	2·31 (s.d. = 0·81)	0·03	0

by the greater mean number of female display movements and the greater proportion of observations which include attacks or chases involving the female. Isolated pairs may be on poorer feeding areas, and may also be more watchful for predators than birds in flocks.

Effect of presence of mate

Feeding rates of females are higher when their mate is close than when he is not (Table 2).

There is a significant difference ($P = 0{\cdot}009$) between the feeding rates of females in each category, and between feeding rate with mate close and close/far ($P = <0{\cdot}1$), and with mate close/far and far/absent ($P = 0{\cdot}05$).

When the mate is close, attacks and chases involving the female occur less often than when the mate is far or absent. However when the mate is close feeding rate is higher despite a greater mean number of female displays. If the feeding rates for females whose mates are close, close/far and far/absent are plotted separately against number of female displays (Figure 2), there is no significant difference between the slopes of each regression line. This suggests that although interactions with other birds always reduce the

Table 2. Female rate and position of mate

Position of mate	no.	Mean feeding rate (items/min.)	Mean no. display movements/min.	% observations with female involved in attacks and chases
Close	79	2·60 (s.d. = 1·06)	1·66	4·3
Close/far	62	2·44 (s.d. = 1·01)	1·23	8·8
Far/absent	95	2·18 (s.d. = 0·90)	0·93	12·2

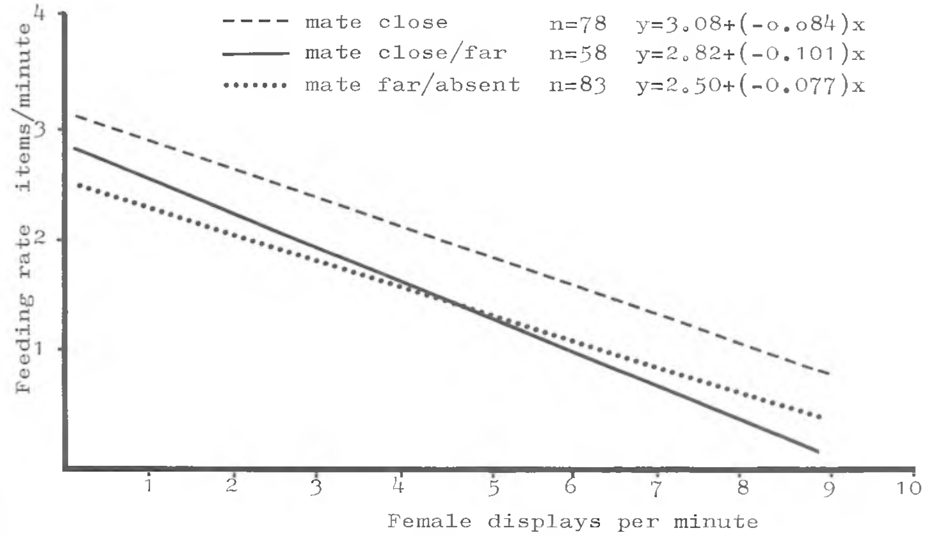

Figure 2. Female feeding rate in relation to number of displays given with each position of mate.

Table 3. Feeding rate of females when male did/did not chase off interfering birds.

	n.	Mean feeding rate (items/min.)	Mean no female displays/min.
Male did	41	2·61 (s.d. = 0·87)	1·53
Male did not	68	2·34 (s.d. = 0·94)	1·57

female's feeding rate, it is higher when the mate is near at every level of interaction. The female may then spend less time watchful and alert and concentrate more on feeding, regardless of how many interactions occur.

A 2-factor analysis of variance of feeding rates in different flock densities and different mate proximities shows no interaction or correlation between these two factors, but that both exert a significant effect on feeding rate. As would be predicted, the highest feeding rates are in medium density flocks with the mate close, and lowest rates are in dense flocks with the mate far away or absent.

The advantage to the female of having the mate present is presumably that he will, if necessary, drive off any interfering birds. Males vary in whether they do this or not. To consider whether it is worthwhile for the female to spend time inciting this response from the male, feeding rate when he does or does not drive off the other bird was compared. The male never failed to respond where the female made a high number of displays, so such observations were not included, giving a similar level of interaction in both categories of male response. Table 3 shows a significantly (P = 0·05) higher feeding rate when their mates responded. Not all the birds the male chased off were males—one third were other females.

Feeding rate of the paired male in the pre-laying period

The feeding rate of adult males at this time is significantly below (P = <0·001) the females' (Table 4). Flock density did not have a significant effect on males' feeding rate. Although the females' feeding rate was on average significantly higher when her mate was close, this is at the expense of the latter's feeding rate (Table 5). The feeding rate of males close to their mates is significantly lower than those close/far or far from their mates (P = 0·04).

The mean feeding rate of males close to their mates in flocks was the same whether or not the male was involved in threatening or chasing off other birds during the observation period. This suggests that the lower feeding rate of males close to their mates is not a direct result of interactions with other birds, but perhaps because he is continually alert and watchful for intruders and must spend time maintaining his position close to the female.

Table 4. Feeding rate of each sex.

Sex	n.	Mean feeding rate (items/min.)
Females	271	2·38 (s.d. = 0·97)
Males	68	2·05 (s.d. = 0·71)

Table 5. Male feeding rate and position of mate.

Position of mate	n.	Mean feeding rate (items/min.)
Close	29	1·79 (s.d. = 0·62)
Close/far	22	2·25 (s.d. = 0·77)
Far/absent	17	2·25 (s.d. = 0·64)

Discussion

In many other duck species the female alone is responsible for the nest, incubation and care of the young, but each season a pairbond is formed, such that the male remains attached to the female after copulation until she is incubating. Kear (1970) lists various species of duck having this system in which the male defends an area round the female. The reasons suggested both for a pairbond and for this aggressive behaviour are reviewed by McKinney (1965). Given that a pairbond is formed, the male may defend an area round the female to prevent other males copulating with her, to prevent interference with copulation, and to strengthen the pairbond. In some species aggressive behaviour may result in spacing out of nests which could have an anti-predator function. Siegfried (1974) suggests that the male Cape Shoveler *Anas smithi* establishes and defends a territory in which the female can feed uninterruptedly before laying.

The results suggest that in the Eider, one function of the pairbond is for the male to protect the female from disturbance by other birds while she is feeding. Interactions in a feeding flock can lower the females' feeding rates considerably, but this effect is significantly reduced if the mate is present and he threatens or chases off intruding birds. The mere presence of the male close to the female gave her some protection from disturbance.

Feeding rate will not be the only factor in obtaining extra food. Item size and quality, and time spent feeding will also be important. However these can only be increased within limits, so higher feeding rates are likely to enhance the efficiency with which females obtain the extra reserves required for breeding.

A positive relationship between the females' feeding efficiency prior to laying and numbers of ducklings subsequently hatched is not yet proven, but, as discussed earlier, seems highly probable. It would therefore be of selective advantage if the male which spends time and energy giving the female protection from disturbance also ensures that the resulting offspring are his by preventing other males from copulating with her. Hence, perhaps, the advantage of monogamy and formation of a pairbond in the pre-laying period. Since pair-formation begins in September, advantages gained by forming a pairbond may begin to accrue some time before laying.

Males varied in the extent to which they were successful in reducing disturbances to their feeding mates. Clearly, if the male were to chase away other birds before they could interrupt the female's feeding (as some were occasionally observed to do), then the female's feeding efficiency would be increased still further. A weak pairbond would mean that the male would spend less time close to the females, moreover the male must also devote some time to feeding himself and males do have higher feeding rates when not close to their mates. The quality of the male and the strength of the pairbond may therefore be as important as the quality of the female in determining her breeding performance.

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Summary

The male Common Eider *Somateria mollissima* plays no part in the care or protection of nest, eggs or ducklings. Despite this, the male forms a pair with a female to whom he remains closely attached for a period prior to laying. One function of this pairbond is for the male to protect the female from disturbance by other birds while she is feeding. She must form a clutch of large eggs, and lay down sufficient fat reserves to maintain her through the incubation period. Interactions with other birds in feeding flocks lower the female's feeding rate significantly, but this effect is reduced if her mate chases off intruding birds. Mere presence of the male close to the female gives some protection from disturbance and increases her feeding rate.

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