Sexual behaviour and plasma androgen concentrations in the male eider duck (*Somateria mollissima*)

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Summary. Eider ducks showed clear tidal and seasonal cycles of display when involved in pair-formation behaviour. Plasma androgen (testosterone and dihydrotestosterone) concentrations did not follow similar tidal cycles but there was a 4-fold increase of androgen in spring when rates of display increased 2-fold. There was no difference in androgen levels in blood samples taken from paired birds before and after coitus. Androgens therefore appear to be essential for the expression of sexual behaviour, but there is no apparent quantitative correlation between overt sexual activity and androgen concentrations.

Introduction

Most birds living in temperate zones exhibit daily and seasonal cycles of sexual behaviour and the immediate cause of such cycles is of interest. Sexual behaviour in the male is usually dependent for its expression upon the presence of testosterone (see Hutchison, 1970), and it is often assumed that any fluctuations are due to underlying changes in testosterone levels. However, little information exists on the exact relationship between levels of testosterone in the blood and the overt expression of sexual activity, particularly for wild birds in natural conditions.

In the eider duck (*Somateria mollissima*), the period of overt sexual activity is prolonged, with pair formation displays beginning in September and continuing until all the females are incubating in June (Gorman, 1974). The disparate sex ratio (1.2 ♂/♀), the fact that the male takes no part in incubation or in parental care, and his promiscuity all ensure that a substantial proportion of the males are involved in pair formation throughout this period. Such pairing results from social courtship, in which up to 30 males display around a single female. The formation of a pair probably results from the choice, by the female, of one of the males displaying around her (McKinney, 1961).

The species is therefore suitable for an examination of the correlation between behaviour and androgen levels. The concentrations of androgen were also studied, before and after coitus, in paired birds.

Materials and Methods

The birds studied were those of a wild population of eider ducks associated with the Ythan estuary, Aberdeenshire, 58°N, 2°W.

Sexual behaviour

Ten ritualized displays are used by the male eider duck in its sexual behaviour. All are used during pair formation and during the precopulatory sequences of established pairs, although the relative frequency of occurrence of each differs in the two situations (McKinney, 1961; Gorman, 1974). Five of the displays, cooing movements 1, 2 and 3, wing-flapping and bathing, were used in the present study for measurement of daily and seasonal changes in the rate of display during pair-formation sequences.

Daily cycle. Pair-formation display is restricted to the hours of daylight (Gorman, 1970). The incidence of the five displays in pair-formation sequences was recorded for a total of 30 non-consecutive days between October 1973 and February 1974. From twilight to twilight, on each of these days, observations were made for 10-min intervals followed by 5-min gaps, and the total number of displays given by a group of about 20 birds was counted. An average rate of display, expressed as displays/bird/min was then calculated for each 10-min interval and for longer periods of time.

Seasonal cycle. Tidal movements proved to be the major influence on the diurnal pattern of display (see below). Consequently, when measuring seasonal changes in display rate, observations were made only during flood tides and only on days when the whole flood tide occurred during daylight hours. Counts of displays were made in the way described for the daily cycle, and average rates were calculated for each flood tide.

Plasma testosterone

A total of 271 samples were obtained from shot or trapped birds. Moulting birds, and birds in eclipse plumage, were shot at sea between the Ythan and Don rivers. All other birds were shot or trapped on the Ythan estuary. All samples were taken between 10.00 and 14.00 h, but at various stages of the tidal cycle. A number of paired birds was shot immediately before, or at known times after, copulation. Those shot before copulation were each displaying around a prone, receptive female and coitus would have followed within 1–5 min.

Blood was removed from the femoral vein and collected in heparinized tubes. Plasma was separated and stored at -70°C until assay. The plasma samples were extracted with redistilled diethyl ether and the extracts dried under nitrogen. The completeness of extraction was checked by extracting five 25 μl aliquots of the [^3H]testosterone tracer from plasma samples with ether and counting the dried residues. The results were corrected for the efficiency of extraction (96.4 ± 2.3 (S.E.M.)%). The testosterone concentrations in the extracts were measured, without purification, by a radioimmunoassay with the CEA-IRE-SORIN antiserum (conjugate of testosterone-3-(O-carboxymethyl)-oxime with bovine serum albumin raised in New Zealand White rabbits: Eurotope Services, London N.12). This antiserum reacted appreciably only with dihydrotestosterone (75%): all other steroids tested (androstenediol, androstenedione, androsterone, epitestosterone, dehydroepitesterone, progesterone, oestradiol and cortisol) gave cross reactions of $<0.2\%$ (manufacturer's figures). The assay thus measured testosterone and dihydrotestosterone and the measurements are referred to as androgen concentrations. The binding ability of the antiserum was 48%. The calibration curve was established for known amounts of testosterone (12.5–400 pg/tube) in the residue of 2 ml diethyl ether present in each tube. All samples were assayed in duplicate; the intra-assay variation was $4.81 \pm 0.39\%$. The inter-assay variation for 30 different plasma samples run in 3 assays gave a mean variation of $9.4 \pm 2.7\%$. The sensitivity of the assay, the smallest amount of testosterone significantly different from zero, was 28 pg/tube or 10 ng/100 ml plasma.

Results

Sexual behaviour

Daily cycle. During the hours of daylight, the tidal movements of the Ythan estuary were the dominant influence on the pattern of activity of the birds, which moved down the river on the ebb tide, stopping to feed on mussels (*Mytilus edulis*) as they became exposed. Feeding ceased soon after low water and the birds moved up river again, carried by the flood tide. The period around high water was spent in roosting and preening. This tidal pattern of movement persisted throughout the night.

To assess the influence of this tidal rhythm of activity on the rate of display in the population, each of the 30 days of observation were divided into four parts: 1 h each side of low water, 1 h each side of high water, and the intervening flood and ebb tides. The mean rate of display for each of these periods was then calculated using the data from all 30 days. The results are shown in Text-fig. 1.

The influence of the tidal cycle on the rate of display is clear; the mean rate on the flood tide was greater than that on the ebb tide ($P < 0.001$) while high water was a period of relative inactivity. Display rates at the time of low water were greater than those on the ebb tide ($P < 0.01$) but lower than those on the flood tide ($P < 0.02$).

Text-fig. 1. Mean display rates (see text) and plasma androgen levels of eider drakes, sampled between September and February, plotted against the state of tide at which they were collected. The curved line represents an idealized tidal cycle, with high water at 0 and hours before and after.

Text-fig. 2. Seasonal changes in the mean rate of display (see text) in pair-formation sequences of eider ducks. Each value is the mean rate during a single flood tide in 1973-1974 (○) and 1974-1975 (●).

Seasonal cycle. Seasonal changes in the rate of display, based on a number of flood tides between 1973 and 1975, are shown in Text-fig. 2. The pattern was essentially similar in both years. Males did not display during moult and the eclipse plumage. Display began in late August and increased, as the autumn progressed, to a clear peak in October and November. After a drop in the rate of display, the new level persisted throughout the winter months, until, in early March, there was a dramatic increase. The high rates of display of March and April dropped abruptly in June as the next moult began.

Plasma androgen

The concentrations of androgen in all the plasma samples obtained are shown in Table 1. The levels varied from undetectable to 200 ng/100 ml. The variations in samples taken at the same time of year were striking and were presumably indicative of episodic release of androgens. Equally striking was the number of samples in each month in which the androgen level was < 10 ng/100 ml, e.g. all samples taken in the period June–August, when males were moulting or in eclipse plumage. During the autumn and winter some of the samples were above 10 ng/100 ml but all were below 50 and most below 30 ng/100 ml. During March, April and May androgens were detectable in most samples, with levels as high as 200 ng/100 ml.

Table 1. Seasonal changes in the plasma androgen concentrations (mean $\pm$ S.E.M.) of male eider ducks

	Months											
	A	S	O	N	D	J	F	M	A	M	J	J
No. of samples tested	9	19	35	22	29	17	20	23	33	21	15	10
No. containing < 10 ng/100 ml	9	18	20	9	16	7	12	4	9	6	15	10
Androgen conc. in samples with > 10 ng/100 ml	—	25	22.5 $\pm$ 2.6	21.0 $\pm$ 2.7	18.6 $\pm$ 1.6	20.9 $\pm$ 3.6	31.9 $\pm$ 6.3	117.3 $\pm$ 15.3	106.4 $\pm$ 13.6	130.8 $\pm$ 17.5	—	—

When plasma androgen concentrations of samples collected between September and February were plotted against the state of tide at the time at which they were collected (Text-fig. 1), no correlation could be seen.

Text-fig. 3. Androgen concentrations in paired eider drakes shot just before, or at known intervals after, coitus in the autumn (O) or spring (●).

The plasma androgen levels of the copulating paired birds are shown in Text-fig. 3. Two major points of interest emerge. Firstly, birds indulging in precopulatory display in the autumn or spring did not have exceptionally high testosterone levels and the range found was similar to that of the population as a whole. Secondly, there was no evidence of a post-coital surge of androgens, at least not within the first 30 min of copulating.

Discussion

Birds in eclipse plumage, or moulting, do not display (Text-fig. 2) and their plasma androgen levels lie below the limit of detection of the assay used in this study. The absence of sexual behaviour is therefore associated with very low levels, or possibly the absence of circulating androgens. Sexual display can be elicited in moulting and eclipse male eider ducks by subcutaneous testosterone implants (Gorman, 1974), and testosterone presumably therefore plays at least a permissive role in the overt expression of sexual display by the male eider duck.

The present results permit an examination of whether there is a quantitative relationship between circulating androgen concentrations and the level of sexual behaviour during daily and seasonal cycles and during copulation.

The daily pattern of display is dominated by tidal movements but there is no evidence of a corresponding cycle of androgen production (Text-fig. 1). The tidal cycle of display appears to be based on the need to feed on the ebb tide and at low water when the mussel beds are exposed. It has not been possible to obtain blood samples from wild birds during darkness, the time when display is absent, but samples taken at night from captive birds are as variable, and fall within the same range, as those taken during the day. The cessation of display at night is not therefore related to reduced androgen levels.

The male eider duck has no clear circadian or tidal rhythm of androgen release related to its activities; the indications are that androgens are released in an episodic manner with no evidence of synchronization between individuals. The lack of relationship between overt display and androgen levels is not unexpected in view of the finding that the brain androgen receptors which mediate sexual behaviour are limited in number and remain bound with testosterone for relatively long periods (Hutchison, 1976). Clearly such a mechanism will tend to damp any possible effects on behaviour of short-term fluctuations in circulating androgens.

Although there were two clear peaks of display rate, one in the autumn, the other in the spring (Text-fig. 2), androgen concentrations remained relatively constant and low from September to February (Table 1). The spring peak of display rate coincided with a rise in androgen levels. In the spring, therefore, display rates were twice as high as those of the autumn while androgen levels increased fourfold. The spring peak of androgen concentration is almost certainly related to the stimulation of sperm maturation because spermatogenesis proceeds beyond the secondary spermatocyte stage at this time (Gorman, 1974), but an effect on sexual motivation also cannot be excluded.

The apparent lack of effect of sexual excitement at copulation on androgen concentrations (Text-fig. 3) may be related to the trauma of killing the birds. In mammals there is much variation in the extent to which testosterone values change following coitus. For example, Fox, Ismail, Love, Kirkham & Loraine (1972) report a post-coital surge of testosterone in man while Stearns, Winter & Fairman (1973) could detect no such relationship. Sexual excitement in bulls clearly leads to an increase in plasma testosterone (Katongole, Naftolin & Short, 1971), but levels in rams are not affected by coitus (Purvis, Illius & Haynes, 1974).

Thus, although the presence of androgens (probably testosterone) appears to be essential for the expression of sexual behaviour, and Gorman (1974) previously indicated a close correlation between the annual cycles of display and of Leydig cell abundance and activity, the results of the present study suggest that there is no quantitative correlation between overt sexual activity and androgen levels. Other facts must therefore be involved in the expression of display behaviour. The effects of the feeding behaviour of the birds on the diurnal rhythm of display have been discussed above. The daily weather is probably an important influence, rain appearing to inhibit and sunshine and frost to

enhance display behaviour. At a seasonal level, the receptivity of the females and the decreasing numbers of females available as the year advances undoubtedly have a major influence on the behaviour of the males.

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