Seasonal reproduction in ewes selected on seasonal changes in wool growth

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Summary. Romney and Perendale ewes were selected on the amplitude of seasonal wool growth. The ewes were fed a constant plane of nutrition and run with vasectomized rams. Ovarian activity was recorded by laparoscopy during 11 months. Ewes with a low amplitude of seasonal wool growth (Group L) had a 68% higher wool growth rate in winter and a 17% lower wool growth rate in summer compared with ewes with a high amplitude (Group H). There was no difference between the groups in the date of the first mating mark. Ewes in Group L entered anoestrum significantly later than did ewes in Group H; the difference was 11 days in the mean date of the last mating mark and 17 days in the mean date of the last ovulation. A significantly higher proportion of ewes in Group L ovulated during July to November. In addition, ewes in Group L had a significantly higher proportion of multiple ovulations throughout the experiment: on average the difference between the groups was 0.21. These results show that phenotypic selection for a low amplitude of seasonal wool growth resulted in a delay in the end of the breeding season associated with an increase in ovulation rate, suggesting independent effects on the beginning and end of the breeding season.

Introduction

Photoperiod is the principal factor determining the length and timing of the breeding season in ewes (for review see Karsch et al., 1984), and within the period of cyclic activity there is a marked seasonal change in ovulation rate (Land et al., 1973; Allison & Kelly, 1979). Therefore, to achieve maximum production, mating must be restricted to a period of 4–6 weeks early in the breeding season when ovulation rate is highest. This represents a major constraint in the organization of sheep management systems.

In addition to the annual cycle of reproduction, there is a marked seasonal pattern of wool growth in long-wooled breeds; summer wool growth rates are typically 3–5 times those in late winter (Story & Ross, 1960; Sumner & Wickham, 1969). There is strong evidence that the seasonal change in wool growth is under the control of photoperiod: the pattern is reversed by reversing photoperiod (Morris, 1961); acceleration of the wool growth pattern or shedding cycle occurs when animals are exposed to alternating periods of long and short days (Hutchinson, 1965; Ryder & Lincoln, 1976; Lincoln et al., 1980; Lincoln, 1984; Lincoln & Ebling, 1985), and exposure to continuous light or dark can lead to the gradual extinction of the previous pattern of wool growth (Hart, 1961; Hutchinson, 1976).

Across breeds there is a positive association between the seasonalities of wool growth and reproduction. For example, the Merino breed that has a long breeding season shows little or no effect of photoperiod on wool growth (Nagorcka, 1979). At the other extreme, primitive breeds such as the Soay have a short intensive breeding season and a pronounced seasonal cycle of wool follicle activity and shedding (Ryder & Lincoln, 1976). No relationships between these parameters have been documented within breeds. The aim of this experiment was to study ewes selected for high or low amplitudes of seasonal wool growth to examine the relationships between seasonal wool growth and seasonal reproduction within breeds.
Animals

Wool growth rates of 280 Romney and 370 Perendale ewes were determined (by mid-side patch clipping) in 8 consecutive 3-month periods (approximating the 4 seasons) from 4 until 28 months of age. In May 1983, 10 ewes with a consistently large seasonal change in wool growth (high amplitude, Group H) and 10 ewes with a consistently small seasonal change in wool growth (low amplitude, Group L) were selected within each breed (total = 40) to study the relationships between the amplitude of wool growth, staple strength and feed intake (Hawker & Crosbie, 1985).

Management

The 40 selected ewes were 4 and 5 years old at the start of the experiment in January 1985. Ewe liveweights were recorded (after an overnight fast) on 8 January, then at 6 weekly intervals until 2 July and at 2 weekly intervals until the end of the experiment on 5 November. Throughout the experiment the ewes were run as one flock outdoors on ryegrass/white clover pastures at the research station (latitude 45°51'S). The ewes were offered a pasture allowance of ~1.2 kg dry matter/ewe/day and the ewes received an allowance of pellets at 0.63 kg dry matter/ewe/day. The mixed diet of pellets and pasture was maintained until the end of the experiment in November. The pellets fed were an equal mixture of two commercial sheep pellets; a high protein pellet consisting mainly of peas (87%), barley (8%) and linseed (5%), with about 20% protein, and a standard pellet consisting mainly of wheat (40%), barley (25%), oats (21%), and wheat bran (10%), with about 12-15% protein.

From the start of the experiment the ewes were run with harnessed vasectomized rams. Every 2 weeks the rams were changed, the harnesses checked, and the crayon colour changed. Crayon marks on the ewes were recorded each week and assumed to indicate that the ewes had been mated. During the mid-breeding season (late May) difficulties were experienced with the brand of ram crayons used. The crayons were harder than previous batches and failed to leave adequate marks. From early June, an alternative brand of ram harness and crayon was used and the soft crayons gave good marks for the remainder of the experiment. Data on mating marks are therefore presented only for the beginning and end of the breeding season.

Ovulation rates were recorded by laparoscopy on 10 April and every 2 weeks from 21 May until 5 November. At laparoscopy the ewes were given an intramuscular injection of Acepromé (1 ml: Syntex Laboratories, New Zealand) and at the sites of puncture of the abdominal wall, 3-4 cm either side of the mid-line, the ewes were given subcutaneous injections of chlorhexidine + lignocaine (Xylocaine, 1 ml: Astra Pharmaceuticals Pty Ltd, Australia). Ovulation rate and mating records were kept for individual ewes until a ewe had not ovulated for two successive laparoscopy observations. In all cases the last mating mark was recorded before the ewes were first recorded as anovulatory at laparoscopy.

Data analysis

Differences between the groups and breeds in ewe liveweight, the dates of first and last mating mark and the date of last ovulation were tested by analyses of variance. The proportion of ewes ovulating and the proportions of those ewes with multiple ovulations at each date of observation were analysed by generalized linear model techniques using a binomial distribution of errors. The proportions of ewes with multiple ovulations were used in the analyses since only 1% of the 338 observations of ovulation rate were of 3 or more ovulations. Significant differences refer to values of \( P < 0.05 \) unless otherwise stated.

Results

Wool growth and liveweights

From 4 to 28 months of age (i.e. before selection), the 20 Group L ewes had, on average, grown 14% less wool in summer (10.8 and 12.4 g/day, s.e.d. = 1.2) and 78% more wool in winter (5.7 and 3.2 g/day, s.e.d. = 0.5) than had the 20 Group H ewes. During the controlled feeding experiments in 1983 and 1984 (see Hawker & Crosbie, 1985), the Group L ewes grew 3% less wool in summer than those in Group H and 47% more in winter. During the present experiment (Fig. 1b), ewes in Group L grew 17% less wool than did those in Group H during January and February (10.4 and 12.5 g/day, s.e.d. = 0.7), but 68% more wool in July and August (4.9 and 2.9 g/day, s.e.d. = 0.4).
Seasonal reproduction and wool growth in sheep

Fig. 1. Ewe liveweight (a) and seasonal wool growth (b) in ewes with minimum (Group L) and maximum (Group H) amplitudes of seasonal wool growth.

Data on ewe liveweights were analysed up to 24 September. There were no significant differences in liveweight between the two breeds throughout the experiment. Ewes in Group H were consistently heavier than those in Group L (Fig. 1a). The differences were significant on 26 February (73.3 kg and 69.1 kg, s.e.d. = 1.8) and on 10 April (72.8 and 68.8 kg, s.e.d. = 1.8), but were small during the rest of the experiment.

Length of the breeding season

There was no difference between the Romney and Perendale ewes in the mean date of the first mating mark (Table 1). Compared with Romney ewes, the mean date of the last mating mark for Perendale ewes was 9 days later and the mean date of last ovulation was 8 days later, but the differences were not significant (Table 1). The mean dates of the first mating mark for Groups H and L were 1 and 2 April respectively (Table 1). In contrast, at the end of the breeding season, ewes in Group H entered anoestrus significantly earlier than did those in Group L as assessed both by mating marks and ovarian observations ($P < 0.025$). The differences between the groups were 11 days for the date of the last mating mark and 17 days for the date of the last observed ovulation. The mean length of the breeding season for Groups H and L was 136 and 146 days respectively.

There was a significant effect of date of observation on the proportion of ewes ovulating ($P < 0.01$). The proportion of ewes ovulating remained above 90% until mid-August and then fell rapidly. By 8 November only 8% of ewes were still ovulating. The effect of breed on the proportion of ewes ovulating was significant ($P < 0.01$, Fig. 2a), with a higher proportion of Perendale ewes ovulating during July to November. The proportion of ewes ovulating also differed significantly between Groups H and L ($P < 0.01$, Fig. 2b). During July to November the proportion of ewes...
Table 1. Mean dates for the beginning and end of the breeding season for Romney and Perendale ewes and for ewes with minimum (Group L) or maximum (Group H) changes in the amplitudes of seasonal wool growth.

<table>
<thead>
<tr>
<th>Ewe breed</th>
<th>First mating mark</th>
<th>Last mating mark</th>
<th>Last ovulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Romney</td>
<td>1 April</td>
<td>17 August</td>
<td>24 August</td>
</tr>
<tr>
<td>Perendale</td>
<td>4 April</td>
<td>26 August</td>
<td>1 September</td>
</tr>
<tr>
<td>Standard error of</td>
<td>3.7 days</td>
<td>4.7 days</td>
<td>6.2 days</td>
</tr>
<tr>
<td>difference</td>
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<tr>
<th>Wool growth group</th>
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</thead>
<tbody>
<tr>
<td>Group H</td>
<td>2 April</td>
<td>16 August</td>
<td>20 August</td>
</tr>
<tr>
<td>Group L</td>
<td>1 April</td>
<td>27 August</td>
<td>6 September</td>
</tr>
<tr>
<td>Standard error of</td>
<td>3.7 days</td>
<td>4.7 days</td>
<td>6.2 days</td>
</tr>
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<td>difference</td>
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Fig. 2. The relationship between date of observation and the proportion of ewes ovulating for (a) Romney and Perendale ewes and (b) ewes with minimum (Group L) or maximum (Group H) amplitudes of seasonal wool growth.

ovulating declined faster in Group H than in Group L (Fig. 2b). At the observation on 8 November, 17% of ewes in Group L were still ovulating while all ewes in Group H were anovulatory.

**Ovulation rate**

The proportion of ewes that had multiple ovulations decreased significantly with time ($P < 0.01$). On 10 April, 97% of the ewes had multiple ovulations and by early September this proportion had declined to 10%. There was a small, but significant, difference between the breeds. Perendale ewes had a consistently higher proportion of multiple ovulations than Romney ewes (56% and 50%, $P < 0.025$). Over the experiment more ewes in Group L had multiple ovulations.
than did those in Group H ($P < 0.01$, Fig. 3). The smallest difference was recorded at the first observation on 10 April when the proportion of ewes with multiple ovulations was highest. On 21 May the proportion of ewes with multiple ovulations in Group L was 100%, while that in Group H had declined to 66%. The difference of 34% between the two groups then was exceeded only at the observation on 13 August when the difference was 38%. There was a small increase in the proportion of ewes with multiple ovulations in Group H in June, coinciding with the change to concentrate feeding. The reason for the increase in both groups in early August is not known.

Fig. 3. The relationship between date of observation and the proportion of ewes with multiple ovulations for ewes with minimum (Group L) or maximum (Group H) amplitudes of seasonal wool growth.

Discussion

These results show an association within breeds of sheep between seasonal patterns of wool growth and seasonal reproduction. The two groups of ewes had been selected on the seasonal pattern of wool growth (Groups H and L with high and low amplitudes of seasonal wool growth, respectively) and compared with ewes in Group H, those in Group L entered anoestrus significantly later (as assessed by both mating marks and ovarian observations) and had a higher ovulation rate.

The small, but significant difference between the Romney and Perendale breeds in the proportions of ewes ovulating is consistent with previous observations. Kelly et al. (1976) studied ewes in this environment and observed that, compared with Romney ewes, the last detected oestrus was 7 days later for Perendale ewes. However, the differences between the wool growth groups were similar for the Romney and Perendale ewes and there were no significant interactions between breed and wool growth group for any of the variables studied.

The difference in ovulation rate between the ewes in Groups L and H was large and consistent considering the relatively small number of ewes involved. Averaged over the experiment, the difference was 0.21. To achieve a similar difference by nutritional manipulation requires a 10 kg difference in ewe liveweight during the mid-breeding season (Allison & Kelly, 1978; Morley et al., 1978; Kelly & Johnstone, 1982). It is possible that the groups may not differ substantially in ovulation rate at the peak of the breeding season and the differences subsequently recorded may result
from a delay in the seasonal decrease in ovulation rate in the Group L ewes. This is suggested from the observations that the smallest difference between the groups occurred in April, and that the proportion of ewes with multiple ovulations in Group H dropped markedly between April and May (Fig. 3). However, the ewes in Group H were on average 4 kg heavier in April and this could have reduced the difference in ovulation rate between the groups at that time. Further observations would be required to determine whether the groups differ in ovulation rate at the peak of the breeding season.

A significant finding of this study was that, in contrast to the difference between the wool growth groups at the end of the breeding season, there was no difference in the onset of the season. This suggests that the timing of the beginning and end of the breeding season can be altered independently. Evidence to support this hypothesis comes from observations on effects of nutrition on the length of the breeding season and from comparisons between different sheep breeds. Effects of nutrition can influence the end (Allison & Kelly, 1979), but not the beginning, of the breeding season (Hafez, 1952). In ewe breeds with an extended season, it appears that selection can either advance the onset or delay the end of the breeding season rather than extend the breeding season in both directions. For example, the beginning of the breeding season is advanced by 1–2 months in Dorset (Hafez, 1952; Kelly et al., 1976; Webster & Haresign, 1983) and Tasmanian Merino ewes (Wheeler & Land, 1977), but the breeding season ends at a time similar to that of other breeds. In contrast, Finnish Landrace (Wheeler & Land, 1977) and Romanov ewes (Land et al., 1973) start the breeding season at the same time as other breeds, but continue to cycle for 2–3 months longer. Furthermore, Finn and Romanov ewes which have a delayed end to the breeding season also have a markedly higher ovulation rate compared to other breeds (Land et al., 1973; Wheeler & Land, 1977). Higher ovulation rates do not occur in the Dorset or Merino breeds which have an early onset to the breeding season (Kelly et al., 1976; Wheeler & Land, 1977). Selection on seasonal wool growth in the present experiment was associated with effects on both ovulation rate and the end of the breeding season, although the magnitude of the effects was smaller than that observed in the Finn and Romanov breeds.

The observation that phenotypic selection within breeds on seasonal wool growth pattern, breed differences, and nutrition can act to modify either the beginning or end of the breeding season (but not both), supports suggestions that the mechanisms controlling the onset and the end of the breeding season may differ (Montgomery et al., 1985). Studies on the control of seasonal breeding in sheep have demonstrated two effects of photoperiod on changes in gonadotrophin release, a seasonal change in LH pulse frequency in the absence of steroid feedback ('direct photoperiodic drive') and marked seasonal variation in the sensitivity to steroid feedback (for reviews see Lincoln & Short, 1980; Martin, 1984; Karsch et al., 1984). The exact role of the two effects in the control of the beginning and the end of the breeding season remains to be determined.

In conclusion, phenotypic selection on seasonal wool growth patterns increased ovulation rate and delayed the end of the breeding season. Models for the control of seasonal breeding must take account of differences within and between breeds resulting in independent effects on the beginning and end of the breeding season and associated changes in ovulation rate.

We thank Ian Scott for assistance with the management of the animals and Roger Littlejohn for advice with the statistical procedures.

References


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Received 19 May 1986