Inhibitory effect of increased photoperiod on wool follicle growth

A J Pearson, A L Parry1, M G Ashby, V J Choy, J E Wildermoth and A J Craven1

AgResearch, Raukura Research Centre, Private Bag 3123, Hamilton, New Zealand and 1AgResearch, Flock House Agricultural Centre, Private Bag 1900, Bulls, New Zealand

(Requests for offprints should be addressed to A J Pearson)

Abstract

The relationships between circulating prolactin (PRL), wool follicle growth and daylength were investigated in 24 New Zealand Wiltshire ewes housed indoors from September 1989 to May 1991. Twelve control (C) ewes were maintained under natural photoperiod. Two other groups were held in short days (SD; 8 h light: 16 h darkness) commencing from the winter solstice (22 June 1990) for either three (group SD3, n=7) or six (group SD6, n=5) months before reversion to natural daylength. Skin was sampled at one- to four-week intervals for histological determination of percentages of growing primary and secondary follicles. Hourly blood samples over 24 h were collected via jugular cannulae from C sheep in March and July and then monthly from all animals until December 1990 for estimation of mean monthly PRL concentrations for each treatment group. Between autumn (March 1990) and winter (July) primary follicle activity (PFA) and secondary follicle activity (SFA) declined in C ewes (PFA: 97 to 43%, SFA: 100 to 57%). Follicle regrowth during July and August in eight C ewes preceded the initial rise in plasma PRL from the winter minimum (1.6 ng/ml). Across the three groups, four instances of decreased follicle activity were observed, closely following or concurrent with increases in plasma PRL concentrations. The resumption of spring growth in four C sheep was temporarily checked by falls in follicle activities during September and October as PRL concentrations began to increase (3.4 to 8.9 ng/ml). Follicle activity also declined in November and December in eight C sheep, coincident with the rapid rise in PRL to a seasonal maximum in late November (165.4 ng/ml). The increase in SD3 follicle activity over spring was not delayed by short days but during October, after release from treatment, PRL concentrations rose (1.8 to 12.0 ng/ml) and follicle activity declined (PFA: 65 to 38%, SFA: 68 to 43%). In SD6 ewes, PRL concentrations were suppressed (2.1 ng/ml) and relatively constant levels of follicle activity (PFA: 73%, SFA: 95%) were maintained throughout short-day treatment. Release of SD6 ewes into summer photoperiod in January 1991 temporarily interrupted follicle growth (PFA: 68 to 17%, SFA: 96 to 19%) and caused out-of-season shedding in March and April. Contemporary C follicle activities were high (PFA: 95%, SFA: 98%). These data suggest that natural and experimental increases in daylength have a short-term inhibitory effect on growing wool follicles which could be mediated through rising concentrations of plasma prolactin.


Introduction

Seasonal plasma prolactin (PRL) variations in spring and autumn appear to play important roles in the control of pelage growth cycles, as well as in reproduction, behaviour, growth and metabolism (Lincoln 1989). In arctic- and temperate-zone mammals, plasma PRL concentrations are low in winter, high in summer (Ravault 1976, Martinet et al. 1982, Lincoln 1989) and can be varied experimentally using melatonin (Martinet et al. 1983, Lincoln & Ebling 1985) or by photoperiod manipulation (Lincoln et al. 1978, Nagy et al. 1993).

Follicle recrudescence during the spring has been linked to increasing photoperiod and plasma PRL concentration in a variety of species including mink (Allain et al. 1981, Martinet et al. 1983), goats (Henderson & Sabine 1992, Dicks et al. 1994), lemmings (Nagy et al. 1993) and deer (Loudon et al. 1989). Seasonal and experimentally-induced increases in circulating PRL have also been positively correlated with wool growth in some sheep breeds (Lincoln & Ebling 1985, Lincoln 1991). In sheep with highly seasonal pelage cycles, including the Wiltshire Horn (Ryder 1969) and the Mouflon (Ryder 1973), wool follicles commence regression (catagen) after the autumnal equinox prior to an extended period of quiescence (telogen) in winter and spring. Renewed follicle growth (proanagen) and fleece shedding does not occur until the vernal equinox or later. Increasing day length in the six
months following the winter solstice has been proposed as the signal for follicle growth initiation with a species- or breed-dependent variation in the timing (Ryder 1966, 1969, Lincoln 1991).

The interpretation of the existing literature is hampered because follicle growth assessment has been based on indirect observation of shedding patterns or insensitive measures of the length or weight of fibre produced over comparatively long time intervals. Since the dearth of histological data on seasonal pelage replacement was noted by Ling (1970), few new studies have been published. Hence, an experiment was undertaken to clarify the relationships between the annual cycles in wool growth, follicle activity and plasma PRL in New Zealand Wiltshire sheep. These sheep have a seasonal cycle in follicle growth associated with conspicuous fleece shedding in the late spring (Parry et al. 1991). The incomplete entry of New Zealand Wiltshire follicles into telogen during winter, and the brevity of the resting phase, resemble follicle growth cycles in the Shetland (Ryder 1971a), Masham (Ryder 1956) and the Soay (Ryder 1971b) breeds rather than the Wiltshire Horn. This difference is likely to be a consequence of the crossing of Wiltshire Horn and Poll Dorset breeds to form the commercial flock from which our experimental animals were drawn (Parry et al. 1991).

A control group was maintained in natural photoperiod. Two other groups were subjected to either three or six months of short days, commencing from the winter solstice, to test the hypothesis that rising spring PRL concentrations are necessary for follicle regrowth after a period of winter inactivity. The results do not support a direct stimulatory effect of PRL on spring fibre growth in this genotype. Instead, the follicle responses suggest that increasing PRL is initially inhibitory to wool growth.

Materials and Methods

Experimental animals, diet and housing

The experiment was undertaken at the Wallaceville Animal Research Centre, Upper Hutt, New Zealand (51°S, 142°E). Twenty-four, 1-year-old, non-pregnant New Zealand Wiltshire ewes showing some degree of fleece shedding were selected from a commercial flock in September 1989. The sheep were housed indoors in six separate rooms, each exposed to natural light through an exterior window, for 20 months until May 1991. The diet comprised pelleted lucerne (480 g/head per day), pea concentrate (190 g/head per day) and meadow hay ad libitum. The level of feeding in the latter half of the experiment was reduced by 20% to limit the rate of live weight gain.

Experimental protocol

Ewes in three rooms were maintained under natural light for the duration of the trial (group C, n=12). Ewes in 2 other rooms were subjected to 3 months of short days (8 h light:16 h darkness; 8L:16D) from the winter solstice (22 June to 30 September 1990) using exterior window shutters (group SD3, n=7). A third group was similarly maintained in short days for 6 months from 22 June until reversion to natural photoperiod on 29 December 1990 (group SD6, n=5).

Sampling protocol

All sheep were weighed at monthly intervals over the trial duration. In November 1989 a 10 x 10 cm area was marked on the right midside of each sheep with the aid of a template. The wool within this patch was removed with Oster small animal clippers and reshorn every two months until January 1991. The wool samples were washed and weighed under standardised atmospheric conditions (20 °C, 25% relative humidity). The mean fibre diameter was measured (Lynch & Michie 1976) in wool collected in November 1989 and in the bimonthly patch clips. Commencing in September 1989 the area of shed fleece for each ewe was drawn on a standard sheep profile at monthly intervals. The extent of shedding was estimated as a percentage of the total profile surface area.

All C ewes were blood sampled in late March 1990 and again in early July 1990. All 24 ewes were then sampled at monthly intervals until 28 December 1990. Additional blood sampling was undertaken in groups SD3 and SD6 on 18 October and 16 November 1990. For each blood sampling session a catheter (Cavafix, Braun Melsungen AG, Melsungen, Germany) was inserted into a jugular vein of each ewe at least 12 h prior to sampling. Blood collection commenced at 0400 h and continued at hourly intervals until 0400 h the following day in order to establish circadian PRL rhythms for a separate study. At night blood sampling was assisted by a dim red light (<1 lux at 10 cm). Ten millilitre blood samples were collected into tubes containing EDTA, the plasma separated by centrifugation and stored at −20 °C until PRL radioimmunoassay. PRL concentrations were derived by averaging the 25 plasma PRL values for each ewe at each sampling date.

Snip biopsies of skin were taken monthly from October 1989 to May 1991 under local anaesthesia from the left midside region of all C sheep. Skin sampling commenced in the SD3 and SD6 groups in June 1990 and continued until January (SD3) or March 1991 (SD6). Additional skin biopsies were taken weekly for four weeks from each of these groups following termination of short days in October 1990 and January 1991 respectively.
Skin histology

Skin biopsies were fixed in phosphate-buffered 10% formalin, processed through an ethanol/toluene gradient and wax embedded. Serial transverse skin sections of 8 μm were cut and stained by a modified Sappic procedure (Nixon 1993). In each skin sample approximately 20 primary and 85 secondary follicles (in contiguous follicle groups) were examined and classified as growing (anagen) or resting (telogen), according to the method of Nixon (1993). The percentage of anagen follicles was calculated for each follicle population (primary (PFA) and secondary (SFA) follicle activities).

Prolactin radioimmunoassay

Ovine PRL was assayed using ovine PRL (NIDDK-oPRL-I-2) for standards and radiiodination, and ovine PRL antiserum (NIDDK-anti-oPRL-2). PRL was iodinated by the Iodogen technique (Pierce, Rockford, IL, USA), using [125I]iodide (New England Nuclear, Wilmington, DE, USA; NEZ0033A). The assay method was essentially as prescribed for the NIDDK reagents. Separation of antibody-bound label from free label was by second antibody precipitation using excess sheep anti-rabbit serum (generated at the Ruakura Research Centre, Hamilton, New Zealand). Sensitivity was 0·6 ng/ml. Interassay and intra-assay variations at 30 ng/ml were 9·3% and 9·0% respectively.

Statistical analysis

Repeated measures analysis of variance was used to analyse time series data. PRL data were log transformed before analysis. Data are expressed as means ± s.e.m. The PFA and SFA data from each ewe were examined to identify periods of declining activity between July 1990 and March 1991. Short-term declines in follicle activity were tested by comparing each member of a sequence with the percent activity immediately prior to the decline, and calculating the Pearson chi-square statistic. To reduce Type I errors, a decline was only regarded as real if the first value of the statistic exceeded the tabled 5% chi-square value, or the second that at 2·5%, or if any later value exceeded that at a probability value equal to the fraction of 5% corresponding to the position in the sequence. Treatment group average wool production between July and December 1990 (encompassing the SD6 short day period) and changes in mean fibre diameter between October and December 1990 were compared by analysis of variance.

Results

Live weight

Mean live weights increased from 37·9 ± 0·8 kg in September 1989 to 62·9 ± 1·3 kg (P<0·001) in April 1990 as the ewes matured. A further weight gain to 73·1 ± 1·7 kg (P<0·001) had occurred by the end of the trial in May 1991. There were no treatment effects.

Plasma prolactin

Plasma PRL concentrations followed the expected seasonal pattern in the C group (Fig. 1). During the imposition of short days from June, PRL concentrations remained low in the SD3 and SD6 groups. While PRL did not differ between groups on 1 August, concentrations in C ewes had increased above short day ewes by the 30 August (3·4 ± 1·2 vs 1·2 ± 0·5 ng/ml, P<0·01) and by 29 September had increased further (8·2 ± 1·5 vs 1·3 ± 0·4 ng/ml, P<0·01). By mid-October plasma PRL in the SD3 group (now exposed to natural photoperiod) was greater than in the SD6 group (12·0 ± 3·7 vs 2·3 ± 0·8 ng/ml, P<0·001). There was no difference in plasma PRL concentrations between the C and SD3 groups at any sampling date from October to December inclusive. SD6 PRL concentrations remained low by comparison to C (P<0·001) over this period. An unexplained, elevated PRL value from an SD3 ewe (W179) during short-day treatment (65·8 ng/ml, 29 September) was excluded from the analysis.

Follicle activities

The percentage of active primary follicles differed (P<0·01) between treatment groups in June immediately prior to the imposition of short days (Fig. 2). Follicle activities were highest in the SD6 (84 ± 9%) and lowest in the C group (46 ± 9%), with the SD3 group being intermediate (71 ± 8%). The difference had disappeared by August when the percentage of anagen follicles had increased in the C group but not in the short day groups. Eighteen days after release of the SD3 group into natural photoperiod on 30 September, PFA had fallen from 65 ± 12% to 38 ± 14% (treatment group difference P<0·02). Subsequently, activity increased reaching 74 ± 8% by late spring (November 1990) when it did not differ between groups. In SD6 ewes under short-day treatment comparatively constant levels of follicle activity (PFA: 73 ± 3%, SFA: 95 ± 1%) were maintained. In January 1991, within 3 weeks of release of the SD6 group into the prevailing midsummer daylength, SD6 PFA fell from 68 ± 1% to 17 ± 7% (P<0·01). The reduction in SD6 PFA, relative to the C group, persisted in February (P<0·001). Nearly all follicles in both groups were in anagen by autumn (March). Within treatment groups, SFA followed a similar pattern to PFA, with an increased proportion of telogen follicles in SD3 (P<0·01) and SD6 (P<0·001) ewes after release from short day treatment (Fig. 2).
Changes in follicle activities of individual ewes

Individual follicle activity data showed four distinct periods of change between July 1990 and March 1991 as described below. In the 48 follicle populations examined (PFA and SFA from 24 ewes) five showed no evidence of declining activity, in forty a single decline was detected and in three secondary populations (one SD6 and two control ewes) two such transitions occurred. Examples of the temporal relationships between plasma PRL and follicle activities in six individual ewes are illustrated in Fig. 3a-f.

Follicle regression in spring (September–October 1990)

Five of the seven ewes in group SD3 exhibited a drop in PFA and SFA in the eighteen days following release into natural photoperiod (e.g. Fig. 3d). Subsequently, rapid re-entry into anagen occurred. During September and October the resumption of follicle growth from winter minima in four C sheep was also interrupted (e.g. Fig. 3e). The average preceding increase in plasma PRL between 1 and 30 August was greater in these four ewes than in the remaining C group (9·7±2·4 vs 2·4±1·1 ng/ml, P<0·01, pooled t-test).

Follicle regression in early summer (November–December 1990)

Nine C sheep showed reductions in follicle activity in early summer which were coincident with or followed the seasonal PRL peak (e.g. Fig. 3b,c). A similar response was noted in the two SD3 ewes that had not responded to the short- to long-day transition during October (e.g. Fig. 3e). Conversely, two of the four C ewes in which anagen was previously interrupted during the spring showed no evidence of declining follicle activities in early summer (e.g. Fig. 3a).

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Follicle regression in summer (January–February 1991)

After release into the summer photoperiod all five sheep in group SD6 showed a marked reduction in follicle activity (e.g. Fig. 3f) followed by an out-of-season shedding. Contemporary follicle activities in C ewes were close to 100% (e.g. Fig. 3a,b,c).

Wool growth and fibre diameter

There was no overall treatment effect on midside clean wool weights. Wool production in all groups increased from early summer (December 1989) to late autumn (May 1990) (0.18 ± 0.02 to 0.55 ± 0.02 mg/cm² per day) (P<0.001) and then declined to 0.27 ± 0.02 mg/cm² per day (P<0.001) in June. Following imposition of short days there was no treatment effect on wool weights at any individual sampling date. However, wool production averaged over the eight months to January 1990 differed between the three treatment groups (P<0.05). SD6 ewes grew more wool than SD3 ewes (0.34 ± 0.03 vs 0.20 ± 0.03 mg/cm² per day) (P<0.05), but neither short-day group differed significantly from the C group.
(0.27±0.03 mg/cm² per day). Mean fibre diameter (Fig. 4) exhibited a pattern similar to that of wool growth. While there was no short-day treatment effect on mean fibre diameters during the experiment, the change in diameter between October and December 1990 differed between groups (P<0.025). Control diameters fell (-0.88±0.18 µm) while those in the SD3 (+0.66±0.82 µm) and SD6 (+0.78±0.38 µm) groups increased.

Wool growth rate and mean fibre diameter in untreated sheep were correlated (P<0.05) in five wool patch samples (r=0.57 to 0.86). In June (r=0.12) and October 1990 (r=0.35) the correlations were low and non-significant.

Wool weight–diameter correlations in the SD6 group were similar to those in the C group until June 1990 but were low through short-day treatment (r= -0.13 to 0.14).

Fleece shedding

Fleece shedding patterns did not differ between treatment groups in the first twelve months. The first shedding had already commenced at the start of the experiment in the spring of 1989 (September). By autumn (April 1990), 83±3% of the trunk had been denuded. Shedding was later in the second year, compared with the first, in all...
groups. The second shed commenced in late spring (November 1990) in the C ewes (treatment group effect $P<0.05$) followed by the SD3 group in January ($P<0.01$) and the SD6 group in March. By late autumn (May 1991) shedding had ceased in all groups. While the extent of shedding in 1991 ($64 \pm 6\%$) was less than in 1990 ($P<0.001$, paired $t$-test) there were no differences between treatment groups.

**Discussion**

Previous investigators have interpreted increasing photoperiod and associated elevated PRL as stimulatory to renewed follicle growth in ruminants (Ryder 1966, Lincoln 1991) and mustelids (Martinet et al. 1992). However, in the present study, follicle growth resumption in most C sheep preceded the seasonal rise in PRL. Short days imposed from the winter solstice suppressed PRL but not follicle recrudescence. These observations suggest that rising PRL in New Zealand Wiltshire sheep is not a prerequisite for follicle regrowth. Furthermore, if PRL is assumed to have a direct effect on follicle growth, then the present data link rising PRL with the entry of anagen wool follicles into catagen. These associations were seen in both C and SD3 sheep in spring and early summer. While blood samples were not collected from the SD6 group after December (because the subsequent follicle responses were not anticipated), the same short- to long-day treatment applied to similar animals in 1992 resulted in a large PRL surge in January and a precipitous decline in follicle activity, as seen in the present experiment (Pearson et al. 1993a).

Despite the distinction we have drawn between different periods and experimental groups, the same endocrine mechanism involving increasing concentrations of PRL may underlie follicle regression during the spring and summer observed in this and subsequent experiments (Pearson et al. 1993a,b, Craven et al. 1994). An inverse association between changes in photoperiod and histologically determined follicle activity is also evident from previous studies involving a semestral cycle of photoperiod variation with Limousine sheep (Rougeot 1961) or red deer (Kay & Ryder 1978). In both experiments, increasing photoperiod, imposed when a high proportion of follicles were in anagen, was followed by declines in follicle activity. Maximum growth was generally resumed before the longest artificial day. These observations are supported by Allain et al. (1986) who reported that artificially increased photoperiod was associated with increasing plasma PRL and declining PFA in Limousine sheep. Short days were characterised by low circulating PRL and a high proportion of anagen follicles (Allain et al. 1986). Similarly, in SD6 ewes, high follicle activities at the imposition of short days were maintained and wool growth was greater than in the SD3 group where a synchronised

![Figure 4: Mean fibre diameter of midside wool plotted at the mid-point of each two-month clipping interval. The ewes were maintained under natural photoperiod (control, ■) or subjected to short days (8L:16D) for either 3 (○) or 6 (□) months from the winter solstice (SD3 and SD6 groups respectively) (open horizontal bars). Points represent group means ± s.e.m. WS = winter solstice, SS = summer solstice.](image-url)
interruption to follicle growth was observed in October after the termination of short-day treatment.

Follicle progression through catagen and telogen, induced by a sudden increase in the photoperiod, was rapidly followed by proanagen, production of a new wool fibre and shedding within eight weeks. Previous experiments with Soay rams, involving short- to long-day transitions, also induced shedding after a similar time interval (Lincoln et al. 1980) which could be extended using exogenous melanotin to suppress the PRL surge (Lincoln & Ebling 1985). Similarly, in New Zealand Wiltshire sheep, temporary PRL suppression using bromocryptine following a short- to long-day transition, results in a corresponding delay in the induced growth cycle (Pearson et al. 1993b). Hence shedding and wool growth stimulation observed after experimentally increased photoperiod, noted by other investigators, are likely to be the indirect consequences of a follicle growth cycle induced by the rise in prolactin concentration.

In C New Zealand Wiltshire sheep, as in other breeds (Ryder 1969, 1971a,b), early summer interruptions to follicle growth were frequently observed as PRL concentrations peaked prior to the longest day. This growth cycle was more apparent in individual ewes (e.g. Fig. 3b,c) than in the C group follicle activity means (Fig. 2) because of variation in timing between animals. Ryder (1969) described follicle growth cycles at this time of the year as 'subsidiary' to distinguish them from the winter decline in follicle activity. However, in those New Zealand Wiltshire sheep with continuous winter wool growth, follicle growth cycling in November–December might be primarily responsible for the annual shedding. Shedding in 1991 was delayed and less complete in comparison to the previous year (which had commenced prior to housing in 1989). Slower and reduced extent of shedding in Wiltshire Horn sheep housed indoors compared with sheep at pasture has previously been noted (Slee 1965). As there is a tendency for the extent of shedding to increase with age (Slee 1959) other factors such as altered nutrition or reduced indoor light intensity may be involved (Slee 1965).

In the C ewes in late winter, and in the SD3 group in spring, proanagen occurred as PRL concentrations were increasing. Follicle regrowth in the C group following the subsidiary cycle in late spring (November), and in the SD6 group in summer (February), occurred against a background of peaking and falling PRL respectively. The resumption of growth in these different circumstances suggests that proanagen and early anagen follicles may be refractory to PRL status. Perhaps significantly in this context, only two C and one SD6 ewe exhibited more than one period of follicle regression between winter (July 1990) and autumn (March 1991).

When follicle growth status is monitored histologically it is possible to estimate the timing and duration of fibre growth cycles (e.g. Rouget 1961, Ryder 1969). Nevertheless some growth cycles in the present experiment may not have been completely tracked, given the present evidence for rapid switching of follicles between activity states, the monthly skin sampling regime, and the limitations of follicle activity scoring in transverse skin sections (Parry et al. 1996). On the other hand, transitory follicle growth cycles, especially those involving primary follicles alone, are much less likely to be detected by visual observation of the fleece or by the weight of clipped wool samples. Although the patterns of annual wool growth and follicle activity were similar among C sheep, short periods of follicle regression, as in the subsidiary follicle growth cycle or in the SD3 group at the termination of short days, were not reflected in significant changes in bimonthly wool growth rate. However, the different pattern of diameter changes between groups seen in October–December 1990 could have risen from the subsidiary follicle growth cycle observed in most control ewes at this time. More frequent wool sampling or the use of sensitive procedures to estimate individual fibre growth rate (Woods & Orwin 1988) are required if short term changes in follicle activity are to be detected in the fleece.

Wool production is a function of the number of active wool follicles, length growth rate, cross-sectional area and specific gravity of the extruded fibres (Woods & Orwin 1988). As anticipated, C midside wool growth rate and mean fibre diameter were correlated in most wool samples. However, this was not the case in either June or October 1990. Rapid, unsynchronised changes in follicle activity involving the winter decline (May–June) and entry into the subsidiary follicle growth cycle (October–November) may have been responsible for disruption of the relationship in these wool samples. Increased variability of fibre diameter and length growth rate are associated with falling wool production (Story & Ross 1960) when normal fibre length–diameter relationships are uncoupled (Woods & Orwin 1988).

Hormonal modulation of seasonal pelage growth is complex, involving interactions between a variety of hormones (Ling 1970). Differences in responsiveness are also evident between follicle subpopulations, topographical locations, species and breeds. Nevertheless, increasing photoperiod in the spring would appear to be the key entrainment mechanism for seasonal pelage cycles in New Zealand Wiltshire sheep, in concordance with results from other species (Ling 1970). If rising vernal PRL has a direct effect on the anagen wool follicle, as these and other data suggest, then the immediate effect appears to be inhibitory. However, growth-stimulatory effects of prolactin on telogen follicles, reported in other species (Dicks et al. 1994), suggest the possibility that prolactin can act at different stages of the follicle growth cycle. Further elucidation of the underlying mechanisms will require an understanding of the regulation of PRL receptors recently localised to the dermal papilla of wool follicles (Choy et al. 1995).
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