

Correlation with changes in horns and pelage, but not reproduction, of seasonal cycles in the secretion of prolactin in rams of wild, feral and domesticated breeds of sheep

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Summary. Seasonal cycles were monitored in groups of wild (mouflon), feral (Soay) and domesticated breeds of sheep (Shetland, Blackface, Herdwick, Norfolk, Wiltshire, Portland, Merino, Soay × Portland and Soay × Merino) living outdoors near Edinburgh (56°N). Changes in the blood plasma concentrations of prolactin and FSH, and growth of the horns and pelage were measured every half calendar month from 1 to 3 years of age. In all breeds there was a clearly defined seasonal cycle in the plasma concentration of prolactin with an 18–66-fold increase in mean values from the nadir in November and December to the peak in May and June. The seasonal increase in prolactin was closely correlated with the seasonal increase in the growth of the horns, both within and between breeds (e.g. time of peak prolactin vs horn growth for 11 breeds, $R = 0.62$, $P < 0.05$). In the mouflon, Soay and some of the domesticated breeds of sheep (Wiltshire, Herdwick and Shetland), the seasonal increase in prolactin was also temporally correlated with the resurgence of growth of the pelage in spring and a conspicuous moult. In the other breeds developed to produce fine wool (e.g. Norfolk, Portland and Merino), there was no clear seasonal change in the pelage and growth continued throughout the year. Comparison between breeds indicated that continuous growth of the pelage was associated with higher plasma prolactin concentrations in winter. The times of the seasonal changes in plasma concentrations of prolactin were not significantly correlated with the corresponding changes in the plasma concentrations of FSH.

The overall results are consistent with a role for prolactin related to the growth of the horns and pelage rather than the seasonal cycle in reproduction. The differences between the wild-type and the domesticated breeds in the pelage represent the effect of selective breeding to produce a long fine fleece which has involved changes in both the seasonal pattern of prolactin secretion and the growth characteristics of the hair fibres.

Keywords: prolactin; FSH; horn growth; wool growth; moulting; pituitary gland; seasonality; genetic variation; sheep

Introduction

Marked seasonal changes in the blood plasma concentrations of prolactin occur in mammals adapted to cold and temperate climates. This includes wild and domesticated sheep (Ravault, 1976; Lincoln, 1989), wild pig (Ravault *et al.*, 1982), roe deer (Schams & Barth, 1982), rhesus monkey (Beck & Wuttke, 1979), blue fox (Mondain-Monval *et al.*, 1985) and mink (Allain *et al.*, 1981). Prolactin concentrations are highest in summer and lowest in winter in all these species which differ in size, reproductive biology and ecology, and the seasonal cycle occurs in both sexes. Experimental

studies in sheep and cattle have shown that exposure to long days or high temperatures stimulates prolactin secretion (Lincoln *et al.*, 1978; Wetteman *et al.*, 1982) and it is probable that in most species the annual cycle in daylength and temperature act together to induce the seasonal changes in prolactin (Lincoln *et al.*, 1989). In addition, there is evidence for sheep and mink that the annual cycle in prolactin secretion constitutes an autonomous rhythm which persists if animals are maintained under constant conditions (Howles *et al.*, 1982; Boissin-Agasse *et al.*, 1988); the effect of seasonal environmental cues is therefore to influence the time of the long-term cycle in prolactin secretion.

In mammals, prolactin acts on many target tissues in addition to the mammary gland (Bern & Nicoll, 1968; De Vlaming, 1979), and there is experimental evidence indicating a functional role for the seasonal changes in prolactin in the control of gonadotrophin secretion, gonadal activity, sexual behaviour, growth, metabolism and changes in the pelage (Lincoln, 1989a). The most convincing evidence relates to the control of the annual cycle in the moulting and regrowth of the pelage, and a causal link between the changes in prolactin secretion and the pelage cycle has been established in at least four species (Djungarian hamster: Duncan & Goldman, 1984a; mink: Martinet *et al.*, 1984; blue fox: Smith *et al.*, 1987; Kashmir goat: Lynch & Russel, 1990). In the Djungarian hamster, for example, suppression of prolactin secretion by treatment with bromocriptine or hypophysectomy favours growth of the white winter coat, while concomitant treatment with exogenous prolactin stimulates moulting and the growth of the agouti summer coat (Duncan & Goldman, 1984a; Niklowitz & Hoffmann, 1988).

The aim of the current study was to establish whether there is a temporal relationship between the seasonal cycle in prolactin secretion and changes in the pelage in sheep. The seasonal changes in the rate of wool or hair growth were measured over a 2-year period in rams of wild (mouflon), feral (Soay) and various domesticated breeds of sheep which differ in the characteristics of the pelage and the occurrence of a spring moult (Zeuner, 1963; Ryder & Stephenson, 1968; Panaretto, 1979). The changes in the rate of horn growth were also monitored since the horn sheath is produced by modified hair follicles (Dove, 1935; Goss, 1983; see Fig. 4). The temporal relationship between the secretion of prolactin and the seasonal cycle in reproduction was also considered, using previously published data on the seasonal changes in the plasma concentrations of FSH; the variation between breeds in timing of the seasonal FSH cycle has been shown to be very closely correlated with the testicular cycle in these animals (Lincoln *et al.*, 1990).

Materials and Methods

Animals. Groups of 4–7 rams of wild (European mouflon), feral (Soay) and domesticated (Shetland, Blackface, Herdwick, Norfolk, Wiltshire, Portland, Merino, Soay × Portland and Soay × Merino) sheep were kept outdoors near Edinburgh (56°N). The animals were obtained as lambs and studied from about 9 months (first January after birth) to 2 years 9 months of age (total of two annual cycles) as described previously (Lincoln *et al.*, 1990).

Every half calendar month a blood sample was collected by venepuncture from the jugular vein of each animal and the plasma separated within 1 h and stored at –20°C. On each occasion the rate of horn growth was measured using the distance from the base of one horn to a reference mark cut into the upper edge of the horn (Lincoln *et al.*, 1980). Every calendar month the growth of the pelage was measured on the side of the neck. For this the hair or wool was clipped from a standard area and weighed (Lincoln *et al.*, 1980) or the length of the predominant fibres was measured using callipers.

Radioimmunoassay. The concentrations of prolactin in the blood plasma were measured by radioimmunoassay (RIA) using the method of McNeilly & Andrews (1974). The lower limit of detection (90% B/Bo) was 0.2 ng NIH-oP-S15/ml plasma, and the intra- and inter-assay coefficients of variation (CV) were 7.1% and 18.5% respectively, based on the mean of low, medium and high quality control samples measured in 23 assays.

The concentrations of FSH in the blood samples were measured by RIA and the results have been published previously (Lincoln *et al.*, 1990).

Analysis. The times of the peak and nadir of the annual cycle in the plasma concentration of prolactin and growth of the horns were calculated for each animal using a three-point moving average for the half-monthly values. This involved calculating the mean value for each three consecutive time points and repeating this throughout the year to determine the time of the maximum or minimum value for each animal. The time was initially calculated as days

relative to 1 January, and the mean for the two annual cycles was used to determine the mean value for each breed of sheep; this was then converted to the date, with s.e.m. expressed in days. The corresponding mean prolactin values at the peak and nadir were also calculated (Table 1). The significance of the differences between breeds for the timing of the peak and nadir of the annual cycle in the plasma concentration of prolactin and for the corresponding values was assessed by ANOVA followed by Newman-Keul's test using the CLR ANOVA program (Clear Lake Research, Houston, TX, USA) run on a Macintosh computer. The significance of the half-monthly changes in the concentrations of prolactin and growth of the horns and pelage in the individual breeds was assessed by ANOVA with repeated measures using the CLR ANOVA program. The linear correlations between the seasonal changes in prolactin and the seasonal changes in horn growth and FSH, and for the breed comparisons were calculated using Cricket Graph Program (Cricket Software Inc, Philadelphia, PA, USA) (Fig. 3). A Spearman rank correlation was used to assess the significance of the relationship between the plasma concentration of prolactin at the nadir of the seasonal cycle and the degree of seasonality in the growth of the pelage for the different breeds of sheep.

Results

Annual cycle in prolactin

The seasonal changes in the concentration of prolactin in the blood plasma are illustrated for specific breeds in Figs 1 and 2 and summarized in Table 1. There was a significant seasonal change in the plasma concentration of prolactin in all breeds ($P < 0.001$, ANOVA), with no difference in the timing and magnitude of the cycle between the two years (yearling vs 2-year-old rams). There was an 18–66-fold increase in the concentrations of prolactin from the minimum in early winter (November–December) to the maximum in early summer (May–June). There were small but significant differences between breeds in the timing of peak and nadir in the seasonal prolactin cycle and in the maximum and minimum concentrations of prolactin at these times ($P < 0.05$, ANOVA). The two extremes were represented by the mouflon rams which had relatively low concentrations of prolactin and a late peak in the annual cycle, and the Merino rams which had high concentrations of prolactin and an earlier seasonal maximum (Table 1).

Annual cycle in growth of the wool

The seasonal changes in the growth of the wool, and the corresponding changes in the plasma concentration of prolactin in the four breeds are illustrated in Figs 1 and 2. The most marked seasonal change in the pelage occurred in the mouflon rams which showed a conspicuous moult of the entire pelage in the spring (see Fig. 4a). In the winter the pelage consisted of a coarse outer coat of pigmented guard hairs and a fine, dense under coat. By December the coat was complete and there was no fibre growth from January to March. Growth of the pelage resumed in April at the time of increasing prolactin secretion, producing a relatively short and sparse summer coat. Growth of the winter coat occurred in the autumn with the rapid development of the coarse outer coat and the growth of the fine under coat; these changes coincided with the seasonal decrease in the plasma prolactin concentrations. The guard hairs of the winter coat on different parts of the body varied in length and colour producing some of the male characteristics, including the black neck mane and white saddle.

Conspicuous changes in the growth of the pelage also occurred in the Soay, Herdwick, Wiltshire and Blackface rams with a seasonal pattern similar to that of the mouflon. In winter, the pelage consisted of coarse and fine fibres forming a dense coat with each breed having its characteristic fibre type and coat colour. As in the wild-type, there was little or no growth of the pelage in winter and resumption of growth occurred in spring (March) at the time of increasing plasma concentrations of prolactin. Regrowth was associated with a partial or complete moult of the old coat. The rate of wool growth increased throughout the summer and was maximum in the autumn when prolactin values were decreasing. The coat of the Wiltshire rams was unusually short and during the summer months there were additional minor periods of moulting about every 2 months before the longer and denser coat developed in the autumn (Wiltshire, Fig. 4).

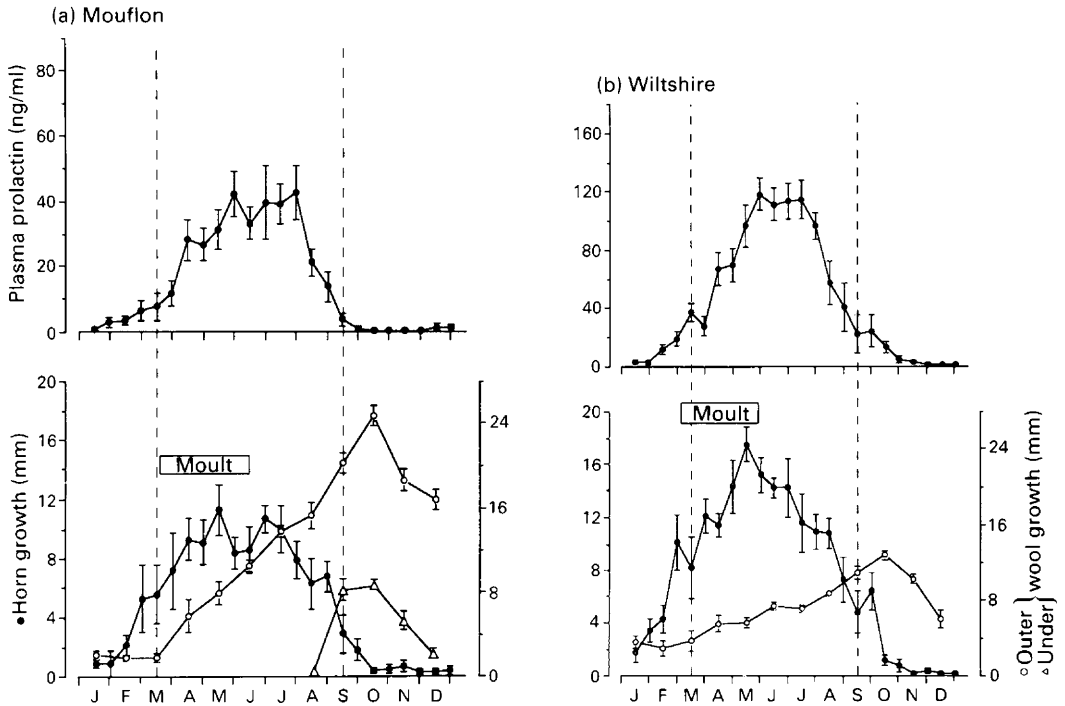


Fig. 1. Seasonal changes in the plasma concentration of prolactin and growth of the wool and horns in mouflon and Wiltshire rams. The values are mean \pm s.e.m., $N = 4-5$, based on samples collected at half monthly or monthly intervals from about 9 months to 1 year 9 months of age. The symbols in the lower panels depict changes in horns (\bullet), course outer wool (\circ) and fine under wool (\triangle), and the period of the major moult of the pelage is indicated (open bar). The vertical broken lines indicate the times of the spring and autumn equinoxes.

In the other breeds of sheep used in the study, the pelage consisted of more uniform fine fibres and there was little or no seasonal change in the growth of the pelage related to the cycle in prolactin secretion (e.g. Norfolk and Merino; Fig. 3). Some growth continued throughout the winter and there was no conspicuous moult in the spring. In the crossbred rams produced by mating Portland or Merino rams with Soay ewes, the appearance of the pelage and seasonal cycle in growth was intermediate between those characteristics of the parents.

The variation between breeds in the degree of seasonality in the growth of the pelage was not significantly correlated with the variation in the plasma concentration of prolactin at the peak of the seasonal cycle ($R = -0.46$, Spearman rank correlation) but was correlated with the concentration at the nadir of the cycle ($R = 0.82$, $P < 0.01$). Very low plasma concentrations between October and December were associated with cessation of wool growth and the subsequent increase in prolactin secretion was associated with reinitiation of growth and a conspicuous moult of the old coat. Higher plasma concentrations of prolactin in the winter were associated with continued growth of the pelage and no moult. The greatest contrast was between the mouflon and the Merino (Figs 1 & 2; Table 1).

Annual cycle in growth of the horns

The seasonal changes in the growth of the horns, and the corresponding changes in the plasma concentration of prolactin in four of the breeds, are also illustrated in Figs 1 and 2. In all breeds there was a significant seasonal change in the growth of the horns ($P < 0.001$ ANOVA). Growth

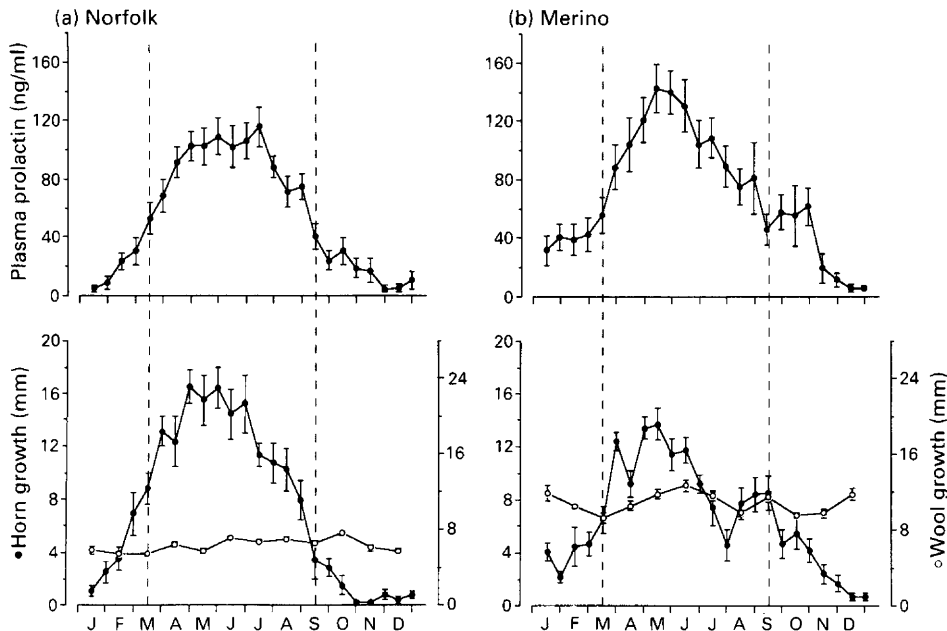


Fig. 2. Seasonal changes in the plasma concentration of prolactin and growth of the wool (○) and horns (●) in Norfolk and Merino rams. The values are mean \pm s.e.m., $N = 6-7$, based on samples collected at half monthly or monthly intervals from about 9 months to 1 year 9 months of age. The vertical broken lines indicate the times of the spring and autumn equinoxes.

was at a minimum from October to January at the time of lowest plasma concentrations of prolactin and increased in spring in parallel with the seasonal increase in the concentrations of prolactin. The small variation between breeds in the timing of the horn growth cycle was significantly correlated with the variation between breeds in the timing of the prolactin cycle (mean time of seasonal peak in horn growth *vs* corresponding value for plasma prolactin for 11 breeds, $R = 0.62$, $P < 0.05$, linear correlation, Fig. 3).

Annual cycle in FSH and testicular activity

There were significant seasonal changes in the plasma concentration of FSH and size of the testes in the different breeds (Lincoln *et al.*, 1990). Of particular note was the variation in the timing of the seasonal maximum in the plasma concentration of FSH, which ranged from late June in the Merino and Portland rams to late September in the mouflon and Herdwick rams. The differences between breeds in the timing of the seasonal cycle in reproduction were not significantly correlated with the variation in the timing of the seasonal cycle in prolactin (mean time of seasonal peak in plasma FSH *vs* corresponding value for plasma prolactin for 11 breeds, $R = 0.34$, linear correlation).

This is illustrated in Fig. 5 for three breeds which differ markedly in the time of the seasonal maximum in plasma concentrations of FSH but not prolactin. In these breeds there was a relationship between the mean concentration of FSH and prolactin at the time of high secretion, but this was not consistent for all breeds.

Discussion

The mouflon represents the wild ancestor of domesticated sheep and in this species the temporal relationship between the seasonal cycle in the secretion of prolactin and growth of the pelage is

Table 1. Summary of the seasonal cycle in the blood plasma concentration of prolactin in rams of different breeds

Sheep breeds	No. of rams	Seasonal maximum		Seasonal minimum	
		Prolactin (ng/ml)	Date	Prolactin (ng/ml)	Date
Mouflon	4	41.60 ± 8.83	24 June ± 10	0.88 ± 0.18	1 Nov. ± 6
Soay	7	115.16 ± 7.46	6 June ± 7	1.91 ± 0.80	2 Dec. ± 6
Shetland	6	117.57 ± 9.80	18 June ± 13	3.99 ± 0.50	22 Nov. ± 14
Blackface	5	156.09 ± 5.53	13 June ± 9	3.16 ± 0.60	2 Dec. ± 5
Herdwick	6	143.76 ± 13.42	19 June ± 8	2.21 ± 0.30	1 Dec. ± 9
Norfolk	6	115.31 ± 10.21	2 June ± 6	6.77 ± 2.53	30 Nov. ± 10
Wiltshire	5	120.48 ± 10.69	18 June ± 7	2.02 ± 0.38	9 Dec. ± 4
Soay × Portland	7	97.10 ± 11.00	22 May ± 7	1.48 ± 0.26	12 Dec. ± 2
Soay × Merino	4	111.08 ± 20.83	10 June ± 8	2.65 ± 0.10	7 Dec. ± 8
Portland	5	165.08 ± 18.65	18 June ± 8	2.74 ± 1.1	5 Dec. ± 8
Merino	7	164.87 ± 10.06	23 May ± 6	4.82 ± 0.98	12 Dec. ± 5

Values are mean ± s.e.m. (see text).

consistent with a functional role of prolactin in the control of changes in the pelage. This could be predicted from experimental studies with other seasonal species for which it has been shown that administration of prolactin to animals in winter pelage causes moulting and growth of the summer coat, while the removal of prolactin from animals in summer results in the development of the winter coat (see Duncan & Goldman 1984a; Niklowitz & Hoffmann, 1988). In the mouflon, there is a conspicuous seasonal cycle in prolactin secretion with a 50-fold increase from winter to summer, and an equally well-defined seasonal cycle in growth and moulting of the pelage between the summer and winter coat, which nicely illustrates temporal relationships. A similar close association between prolactin secretion and the pelage cycle has been noted in other ungulates (Limousine sheep: Allain *et al.*, 1986; Soay sheep: Lincoln & Ebling, 1985; red deer and Père David's deer: Webster & Barrell, 1985; Loudon *et al.*, 1989).

The comparison between the mouflon and the domesticated sheep reveals that the seasonal cycle in prolactin secretion and the seasonal cycle in the growth of the pelage have been modified by selective breeding, and in some breeds there is no longer a clear functional association. This is particularly evident in the breeds developed for their fine quality wool such as the Merino and the Norfolk. In these, the pelage consists of long fine fibres and there is no obvious distinction between a coarse outer coat and a fine under coat, and no difference between the fibre type produced in summer and winter. The fleece continues to grow throughout the year unlike the wild type, and there is no moult in the spring. The Soay, which represents an early stage of domestication, is similar to the wild mouflon in the seasonality of the pelage, while breeds such as the Herdwick and the Wiltshire show intermediate characteristics with a seasonal cycle in growth of the pelage and

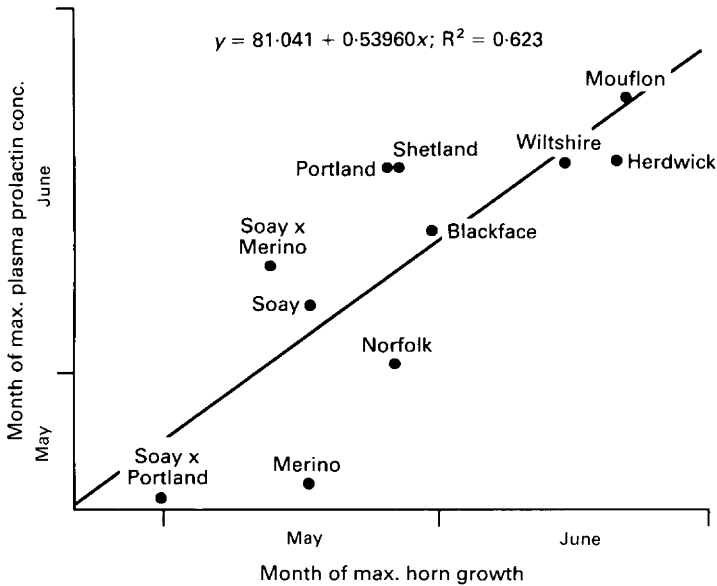


Fig. 3. Correlation between the time of the seasonal maximum in the blood plasma concentration of prolactin and the seasonal maximum in growth of the horns for 11 breeds of sheep.

some aspects of a spring moult (see also Ryder & Stephenson, 1968; Ryder, 1971, 1973; Panaretto, 1979). Since all the breeds show a clearly defined cycle in prolactin secretion, it follows that selective breeding for a uniform long fleece has modified the hair follicles and their response to prolactin. However, changes in hormone secretion may also contribute to the effects since the breeds of sheep showing the least seasonality in the growth and moulting of the pelage had higher circulating concentrations of prolactin in winter. The continued release of prolactin at this time may promote hair follicle activity resulting in continuous growth of the coat in the winter and no spring moult. A similar situation occurs in the seasonal Soay sheep in which the photoperiodic response has been blocked by pinealectomy; prolactin secretion is increased in winter and there is a corresponding increase in wool growth at this time and a less defined spring moult (Lincoln *et al.*, 1989; G. A. Lincoln, unpublished results). This effect of pinealectomy has also been studied in Limousine sheep kept under artificial light cycles in which the growth of the kemp fibres normally occurs during low prolactin secretion (Allain *et al.*, 1986);

Seasonal moulting involves a synchronization of the hair follicles such that the replacement of hair progresses across the body in a wave (Ling, 1972). Histological studies have shown that in mouflon, Soay and some of the domesticated breeds there is a well defined synchronization in the activity of the hair follicles, with all follicles in a resting state in the winter and reactivation occurring in the spring followed by the moult of old fibres (Ryder & Stephenson, 1968; Ryder, 1971, 1973; Panaretto, 1979). In the summer, the length of the growth and resting phase of the individual hair follicles (hair follicle cycle of anagen and telogen) appears to be shorter than in winter as judged by the occurrence of subsidiary cycles of moulting in summer (Panaretto, 1979); this was noted in the Wiltshire rams in the current studies. The thickness or colour of the hair fibres produced by the different types of hair follicles also varies between summer and winter. In the breeds developed for commercially important features of their fleece, the growth characteristics of the hair follicles are very different from the wild-type since the growth phase of the hair follicles is much longer and there is no obvious synchrony amongst the follicles; as a consequence, wool growth appears to be continuous (Ryder *et al.*, 1968). However, minor features of seasonality are often apparent in these breeds; for example, the seasonal moult of hair from the legs in Merino which is

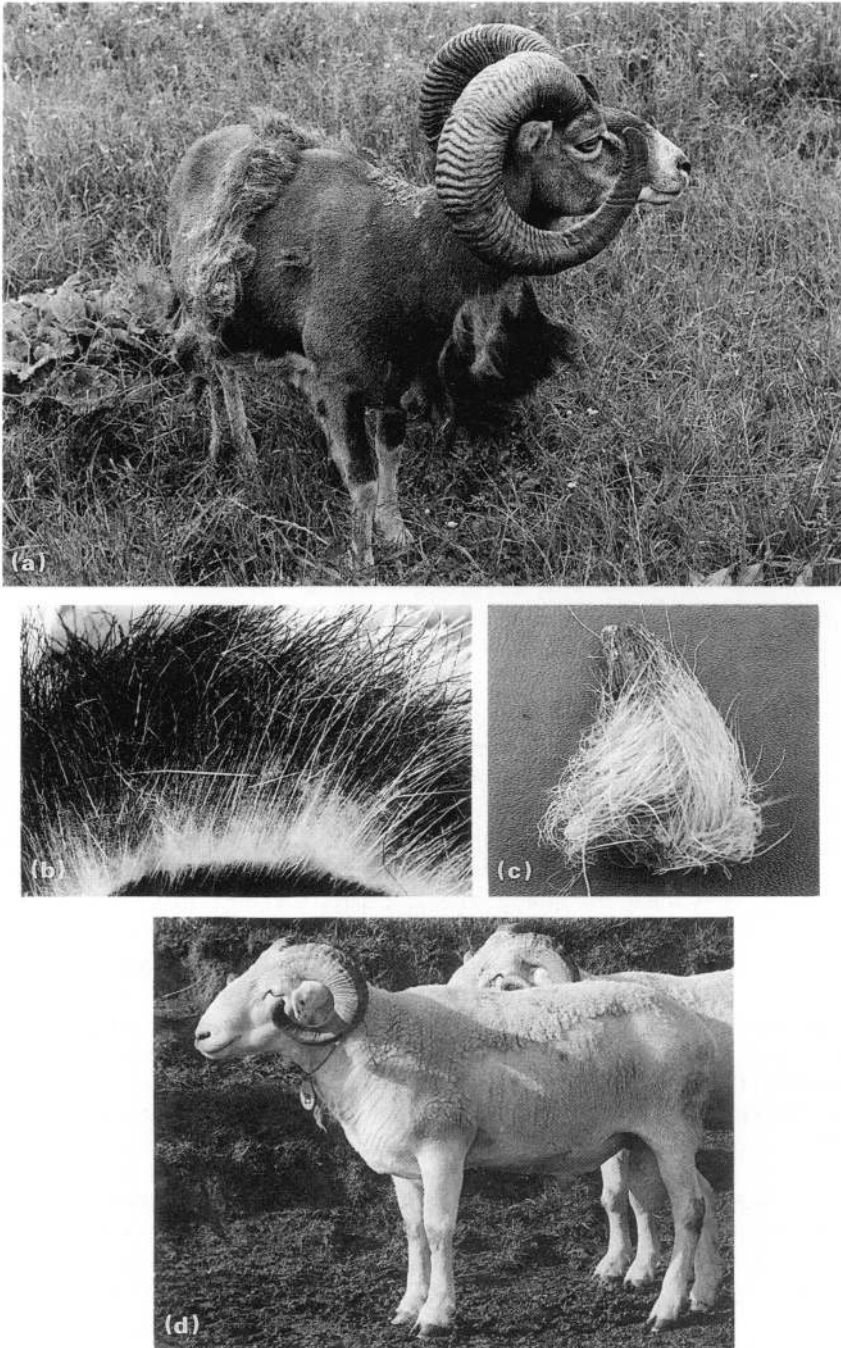


Fig. 4. Photographs relating to the rams used in the current study. **(a)** Mouflon ram in June showing the conspicuous moult of the winter coat and the early development of sparse summer coat. **(b)** Moulded winter coat of mouflon ram showing the coarse outer hair and the fine under hair. **(c)** Accessory horn developed close to the normal horn in one of the Herdwick rams illustrating the close relation between the hair and horn. **(d)** Wiltshire ram in September showing progression of a subsidiary summer moult in this short-woolled breed.

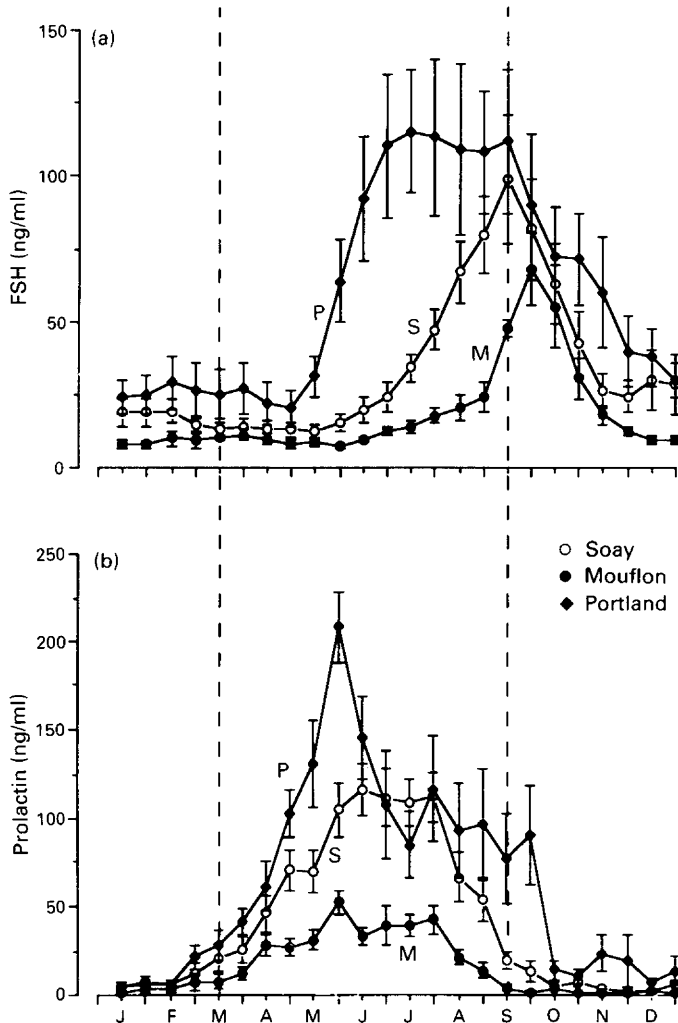


Fig. 5. Seasonal changes in the blood plasma concentrations of (a) FSH and (b) prolactin in Soay (S, ○), mouflon (M, ●) and Portland (P, ◆) rams. The values are mean \pm s.e.m., $N = 4-7$, based on blood samples collected at half monthly intervals from about 9 months to 1 year 9 months of age. The vertical broken lines indicate the times of the spring and autumn equinoxes.

taken to reflect the seasonal ancestry (Panaretto, 1979). While prolactin is implicated in the control of the seasonal pelage cycle, it is not known whether prolactin acts to synchronize the activity of the follicles and/or to promote a short hair follicle cycle and the production of a hair fibre characteristic of the summer. These responses to prolactin appear to be modified or absent in the fine wool breeds.

The pelage is influenced by hormones other than prolactin, including thyroxine which stimulates the rate of wool growth (Girard & Legault, 1969), melanocyte stimulating hormone which promotes melanogenesis (Logan & Weatherhead, 1981; Weatherhead & Logan, 1981) and testosterone which influences the type of fibre produced by hair follicles in specific regions of the body leading to a characteristic male-type pelage (Lincoln, 1989b). The influence of testosterone is relevant to the current study since the observations were made on rams in which there is a marked seasonal cycle in the blood concentrations of testosterone with peak values in the autumn (Lincoln

et al., 1990). In the mouflon, Soay and most of the domesticated breeds, the male secondary sexual features of the pelage, including the growth of a long neck-mane and the development of colour patterns, were developed in the autumn. These changes presumably reflect the influence of the seasonal increase in testosterone secretion by the testes. Testosterone appears to interact with the other hormonal influences on the pelage including prolactin (Duncan & Goldman, 1984b), but it is unlikely that the seasonal testicular cycle dictates the overall pelage cycle since this persists following castration (e.g. varying hare: Lyman, 1943; mink: Rust *et al.*, 1965; Djungarian hamster: Duncan & Goldman, 1984b).

Seasonal changes in the growth of the horns were also evident in the sheep used in the current study; in all breeds growth was maximum in the summer and minimum in the autumn. There was a very close temporal relationship between the rate of growth of the horns and the seasonal changes in the secretion of prolactin both within and between breeds. There have been no experimental studies to test whether prolactin stimulates the growth of the horns in sheep but this seems probable in view of the established effect of prolactin on growth of the pelage. In the mouflon, Soay and the domesticated breeds showing a clear seasonal cycle in the pelage, the resumption in the growth of the horns in spring occurred consistently about 1 month or so before the overt growth of pelage. In the other breeds, the resurgence in growth of the horns also occurred in spring but there was no corresponding change in the pelage. This indicates that the seasonality of the two features is not totally coupled and there are likely to be differences in the way the various hormones influence the horns and pelage.

Testosterone appears to play a particularly important role in influencing the growth of the horns since the large size of the horns is a male secondary sexual characteristic and growth of the horns is largely blocked by castration (Marshall & Hammond, 1913). The seasonal change in the secretion of testosterone is likely to influence the rate of growth of the horns and it has been suggested that high concentrations of testosterone in the mating season actually inhibit growth, allowing the horns to be used for fighting (Goss, 1983). This is consistent with the results of the current study in which growth was minimal in the autumn when the plasma concentrations of testosterone were maximum (Lincoln *et al.*, 1990). However, the resumption of the growth of the horns after the mating season in late winter and spring is not readily explained in terms of a change in plasma concentrations of testosterone. This event is more closely correlated with the increase in the plasma prolactin values which may stimulate the resurgence of growth. The hormonal control of the seasonal cycle in the horns may be similar to that for the antlers in deer in which testosterone plays the major role in dictating seasonal events but there is a separate trophic influence in the spring possibly involving prolactin (Wislocki *et al.*, 1947; Mirarchi *et al.*, 1978).

In this study, the differences between breeds in the timing of the seasonal changes in the plasma concentrations of FSH were closely correlated with the cycle in testicular activity (Lincoln *et al.*, 1990), but not with the variation in the timing of the plasma concentrations of prolactin. This lack of association has been noted in the comparison between other breeds of sheep (Carr & Land, 1982) and amongst species differing in their mating seasons (Lincoln, 1984, 1989a), and this is taken as evidence that seasonal changes in reproduction are unlikely to be controlled by prolactin. This is consistent with studies in sheep and mink in which the long-term cycle in reproduction and prolactin secretion has been shown to dissociate under artificial photoperiods (Worthy & Haresign, 1983; Lincoln, 1989a) or after pinealectomy (Boissin-Agasse *et al.*, 1988; Lincoln *et al.*, 1989), and in the Djungarian hamster there is evidence that the two systems have different critical daylengths (Duncan *et al.*, 1985).

In conclusion, the overall results support the view that prolactin plays a role in the control of the seasonal cycle in the growth of the pelage and horns, rather than influencing reproduction in the rams. The lack of a relationship between the seasonality in prolactin secretion and wool growth in some domesticated breeds is taken to represent the effects of selective breeding for a continuously growing fine wool fleece. A study of the wild-type is recommended to elucidate the mechanisms by which prolactin affects the pelage.

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