Seasonal cycles in the blood plasma concentration of FSH, inhibin and testosterone, and testicular size in rams of wild, feral and domesticated breeds of sheep

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Summary. Seasonal cycles in testicular activity in rams were monitored in groups of wild (mouflon), feral (Soay) and domesticated breeds of sheep (Shetland, Blackface, Herdwick, Norfolk, Wiltshire, Portland and Merino) living outdoors near Edinburgh (56°N). The changes in the blood plasma concentrations of FSH, inhibin and testosterone, and the diameter of the testis were measured every half calendar month from 1 to 3 years of age. There were significant differences between breeds in the magnitude and timing of the seasonal reproductive cycle. In the mouflon rams, the seasonal changes were very pronounced with a 6–15-fold increase in the plasma concentrations of FSH, inhibin and testosterone from summer to autumn, and a late peak in testicular diameter in October. In the Soay rams and most of the domesticated breeds, the seasonal increase in the reproductive hormones occurred 1–2 months earlier with the peak in testicular size in September or October. In the two southern breeds (Portland and Merino), the early onset of testicular activity was more extreme with the seasonal maximum in August. In cross-bred rams, produced by mating Soay ewes (highly seasonal breed) with Portland or Merino rams (less seasonal breeds), there was a seasonal reproductive cycle that was intermediate compared to that of the parents. A comparison between all 11 breeds showed a significant correlation between the timing of the seasonal cycle in plasma FSH concentration and testicular diameter (time of peak FSH *vs* testis, $r = 0.95$).

The overall results in the rams are consistent with a primary role of FSH in dictating the seasonal cycle in testicular size and the secretion of inhibin. The earlier seasonal onset in the testicular cycle in the southern breeds of domesticated sheep, and the differences from the wild type, are taken to represent the effects of genetic selection for a longer mating season.

Keywords: seasonal breeding; pituitary gland; testis; inhibin; genetic variation; sheep

Introduction

All breeds of domesticated sheep are believed to be derived from the Asiatic mouflon, *Ovis orientalis*, living in the mountainous regions from the Mediterranean to Iran (Nadler *et al.*, 1973; Clutton-Brock, 1981). Genetic selection for a longer mating season and greater prolificacy has produced a wide range of breeds which differ from the wild type in their reproductive physiology and behaviour. For example, most breeds of domesticated sheep from colder northern climates have a long period of anoestrus with a short mating season starting as late as November, while breeds from warmer equatorial regions (south of 35°N) have an extended mating season and lambs may be born in all months of the year (Hafez, 1952; Robinson, 1981).

There have been several studies of rams that reveal differences between breeds in various aspects of reproductive physiology and behaviour. There are differences between breeds in the timing and magnitude of the seasonal testicular cycle (Islam & Land, 1977), and seasonal changes in gonado-trophin secretion (Pelletier *et al.*, 1982; D'Occhio *et al.*, 1984), testicular activity and sperm production (Amir & Volcani, 1965; Barrell & Lapwood, 1978/9; Dacheux *et al.*, 1981; Hochereau-de Reviers *et al.*, 1987) and sexual behaviour (Schanbacher & Lunstra, 1976; Poulton & Robinson, 1987). The overall results indicate that the rams of the southern breeds such as the Merino have a less well defined seasonal cycle in testicular activity and sexual behaviour predominantly influenced by seasonal changes in nutrition, while rams of the northern breeds have a marked seasonal reproductive cycle more influenced by seasonal changes in daylength.

The aim of the current study was to extend these observations to compare the seasonal aspects of male reproduction between wild, feral and domesticated breeds of sheep living at one locality. The seasonal change in the pituitary–testicular axis was monitored by measuring the changes in the blood plasma concentration of follicle-stimulating hormone (FSH), inhibin and testosterone. The European mouflon was used to represent the wild type, the Soay sheep to represent the feral type (returned to the wild after domestication) and a range of 7 domesticated breeds of sheep to represent local breeds from different parts of the British Isles and Europe. Cross-bred rams combining extreme seasonal traits were also included in the study. Preliminary results on the seasonal cycle in testicular diameter in all breeds, and the seasonal changes in the blood concentration of FSH and testosterone in the mouflon and Soay sheep have already been published (Lincoln, 1989).

Materials and Methods

Animals. Groups of 4–7 rams of wild (European mouflon), feral (Soay) and domesticated sheep (Shetland, Blackface, Herdwick, Norfolk, Wiltshire, Portland, Merino, Soay × Portland and Soay × Merino) were kept out-doors in grass fields near Edinburgh (56°N) as all-male groups, and given supplementary feeding of hay in winter from December to April. 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). The animal suppliers were The Zoological Society of London, Regent's Park (European mouflon), Mr P. Mapson of Cambridgeshire (Soay, Shetland, Wiltshire and Norfolk), Mr J. Henson of Gloucestershire (Portland and Herdwick) and AFRC Institute of Animal Physiology and Genetics Research of Edinburgh (Boreray Blackface and Tasmanian Merino). Cross-bred rams were produced locally by mating either a Portland ram or a Tasmanian Merino ram with a group of Soay ewes.

Every half calendar month, the diameter of one testis of each ram was measured using calipers (Lincoln & Davidson, 1977). On each occasion a blood sample was collected by venepuncture from the jugular vein and the plasma separated within 1 h and stored at $-20°C$.

Radioimmunoassays. The concentrations of FSH in the blood plasma were measured using a specific ovine radioimmunoassay (RIA) as described by McNeilly *et al.* (1986) using NIAMDD anti-oFSH as first antibody. The lower limit of detection (90% B/Bo) was 0·5 ng NIH-oFSH-S14/ml plasma, and the intra- and inter-assay coefficients of variation (CV) were 10·2% and 23·5% respectively, based on the mean of low, medium and high quality control samples measured in 17 assays.

The concentrations of inhibin in the blood plasma were measured by a newly developed RIA using an antiserum raised in a rabbit to the 1–26 amino acid sequence of the N-terminus of the α-chain of pig inhibin of M_r 32 000 kindly provided by Dr J. Rivier, Salk Institute, La Jolla, CA, USA, and validated for the measurement of inhibin in sheep (McNeilly *et al.*, 1989). The assay cross-reacts with the free α-subunit of inhibin but this has minimal effect on the measurement since the α-subunit is present in low concentrations in peripheral blood of sheep (McNeilly *et al.*, 1989). The sensitivity of the assay was in the range 40–80 pg 1–26 α-inhibin/ml plasma, or 80–160 mU equivalent of ovine follicular fluid standard (oFF CG1083) previously bioassayed in a sheep pituitary cell bioassay against an ovine testicular lymph standard with an arbitrary potency of 1 U/ml (Tsonis *et al.*, 1986). The intra- and inter-assay CVs were 14·6% and 21·8% respectively based on quality control pools measured in 9 assays.

The concentrations of testosterone in the blood plasma were measured by RIA with extraction using the method of Corker & Davidson (1978) modified for an iodinated tracer (Sharpe & Bartlett, 1985). The sensitivity of this assay was 0·1 ng/ml, and intra- and inter-assay CVs were 12·8 and 19·3% respectively.

Analysis. The mean annual reproductive cycle for all breeds was calculated based on data for each animal for the first of the 2 annual cycles for which data were collected (62 rams for the period January to December, about 9 months to 1 year 9 months old) (Fig. 1). The significance of the seasonal changes was assessed by ANOVA using a CLR ANOVA program (Clear Lake Research, Houston, TX, USA) run on a Macintosh computer. The linear correlation between the changes in the blood plasma concentration of FSH, inhibin and testosterone in spring, summer, autumn

and winter was calculated using Cricket Graph Program (Cricket Software Inc., Philadelphia, PA, USA) based on the mean of the hormone concentrations collected every half calendar month for all animals.

The time of the peak and nadir of the annual cycle in the concentration of each of the reproductive hormones and the diameter of the testis was calculated for each animal using a three-point moving average. The time was initially calculated as days relative to 1 January, and the mean for the 2 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 values for the reproductive hormones and the diameter of the testis 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, and for the corresponding values for each parameter was assessed by ANOVA followed by Newman–Keul's *t* test. The linear correlation between the time of the seasonal maximum in the plasma concentrations of FSH and the seasonal maximum in diameter of the testis for all 11 breeds was calculated using the Cricket Graph Program (Fig. 3).

Results

Annual cycle: combined data for all rams

The seasonal changes in the concentration of FSH, inhibin and testosterone in the blood plasma, and the diameter of the testis, using the combined data for all the rams (62 rams of 11 breeds), are illustrated in Fig. 1. There was a significant seasonal change in all parameters ($P < 0.001$, ANOVA), with minimum values occurring in spring (March–May) and maximum values in autumn (September–October). The seasonal increase in the plasma concentration of FSH from June to September occurred in close parallel with the increase in the plasma concentration of inhibin and growth of the testis, while the marked rise in the plasma testosterone values was about 2
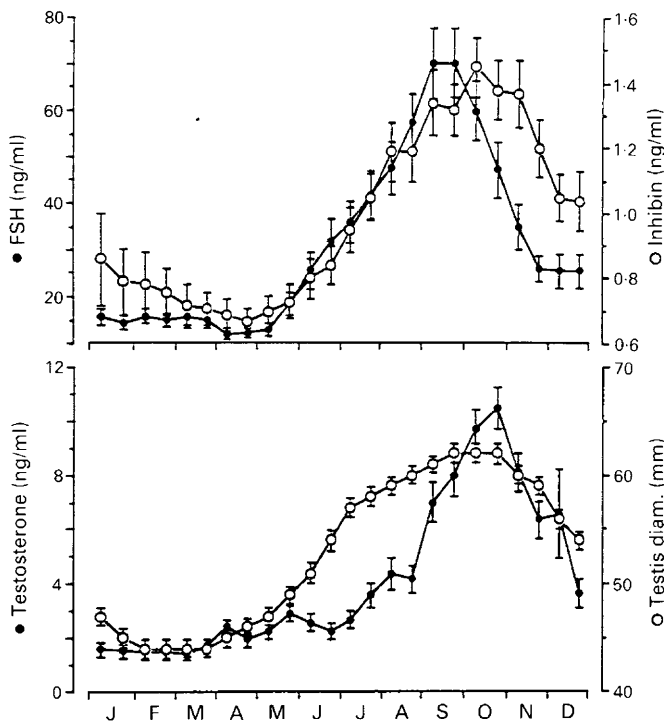

Fig. 1. Seasonal changes in the blood plasma concentration of FSH (●) and inhibin (○), and the blood plasma concentration of testosterone (●) and diameter of the testis (○) in rams living outdoors near Edinburgh (56°N). The values are mean ± s.e.m. for all 62 rams of 11 breeds (see text) sampled every half calendar month from about 9 months to 1 year 9 months old.
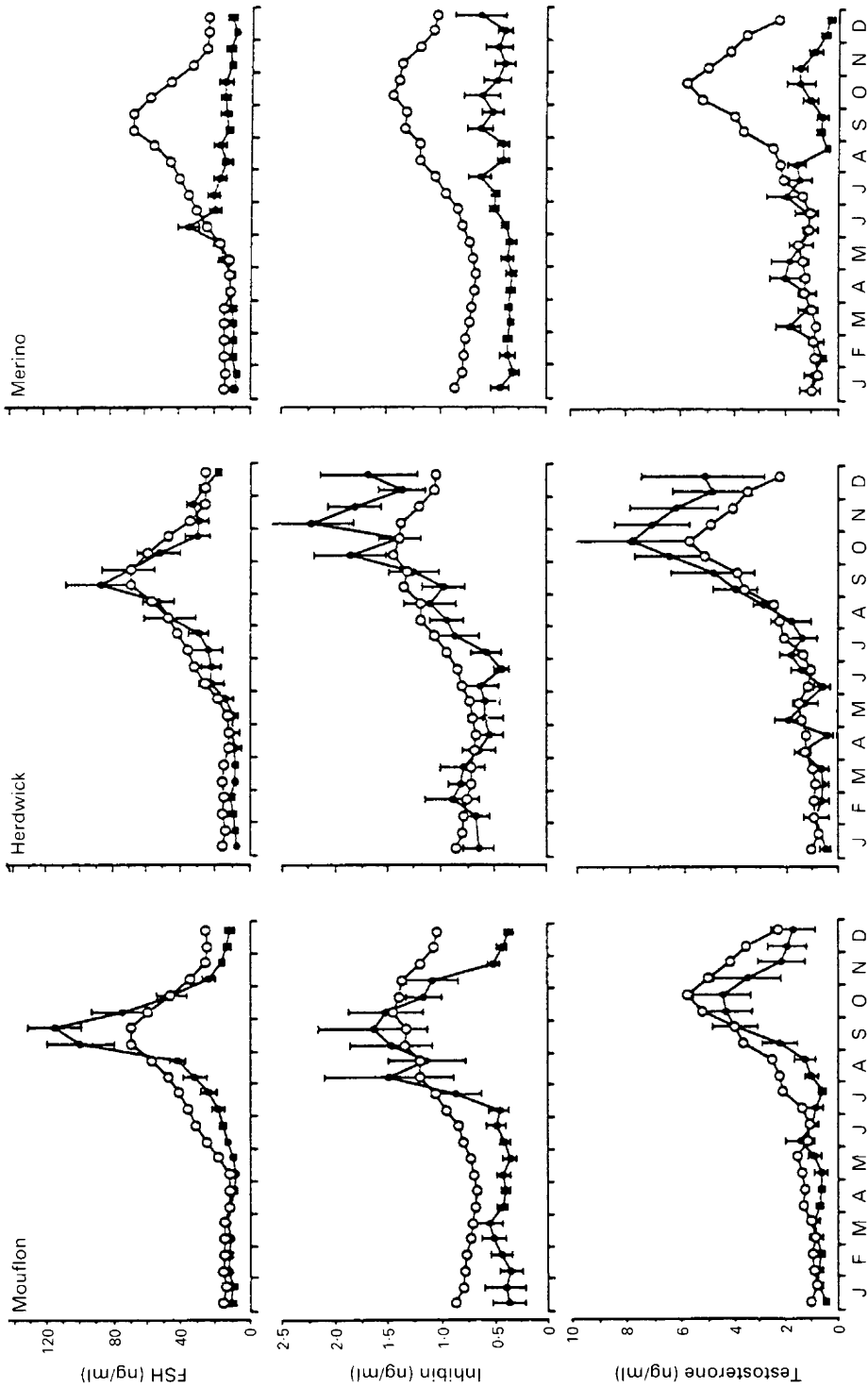
Fig. 2. Seasonal changes in the blood plasma concentration of FSH, inhibin and testosterone in mouflon, Herdwick and Merino rams. The values are mean ± s.e.m., $n = 4–7$ (●) based on blood samples collected every half calendar month from about 9 months to 1 year 9 months old and compared to mean values (○) for all 62 rams of 11 breeds.

Table 1. Summary of the seasonal cycle in the blood plasma concentrations of FSH, inhibin and testosterone in rams of different breeds (aged 1–3 years)

| Sheep breeds	No.	FSH Seasonal maximum FSH (ng/ml)	Date (days)	FSH Seasonal minimum FSH (ng/ml)	Date (days)	Inhibin Seasonal maximum Inhibin (ng/ml)	Date (days)	Inhibin Seasonal minimum Inhibin (ng/ml)	Date (days)	Testosterone Seasonal maximum Testosterone (ng/ml)	Date (days)	Testosterone Seasonal minimum Testosterone (ng/ml)	Date (days)
Mouflon	4	76·8 ±13·4	21 Sept. ±3·4	5·5 ±1·0	3 Apr. ±24·7	1·78 ±0·40	24 Sept. ±9·8	0·30 ±0·06	18 Jan. ±8·3	4·48 ±0·68	17 Oct. ±1·8	0·31 ±0·03	24 Mar. ±11·5
Soay	7	93·7 ±16·1	2 Sept. ±3·9	9·5 ±1·7	11 Mar. ±12·6	1·77 ±0·19	17 Nov. ±5·2	0·37 ±0·05	5 Feb. ±4·7	7·38 ±1·04	27 Oct. ±13·9	0·36 ±0·06	27 Feb. ±8·6
Shetland	6	93·5 ±12·0	31 Aug. ±9·0	15·7 ±1·3	27 Feb. ±8·4	2·21 ±0·45	21 Sept. ±29·8	0·41 ±0·09	8 Feb. ±13·9	8·86 ±0·89	25 Oct. ±3·8	0·63 ±0·09	29 Mar. ±15·6
Blackface	5	73·1 ±11·6	7 Aug. ±6·4	10·7 ±1·9	8 Apr. ±8·8	2·24 ±0·35	26 Sept. ±8·0	0·48 ±0·05	2 Apr. ±17·8	6·98 ±0·43	13 Oct. ±2·8	0·36 ±0·06	22 Feb. ±11·9
Herdwick	6	80·0 ±16·9	7 Sept. ±4·4	7·6 ±0·5	6 Mar. ±10·7	2·14 ±0·21	10 Nov. ±11·5	0·48 ±0·11	14 May ±26·1	8·16 ±0·83	25 Oct. ±9·1	0·29 ±0·07	18 Feb. ±11·9
Norfolk	6	29·3 ±6·0	2 Sept. ±4·1	4·9 ±0·6	9 Apr. ±11·1	2·32 ±0·21	12 Nov. ±32·8	0·97 ±0·09	31 Mar. ±34·1	7·72 ±0·96	16 Oct. ±6·1	0·42 ±0·9	26 Feb. ±12·2
Wiltshire	5	46·4 ±8·8	31 Aug. ±6·1	12·3 ±2·2	6 Apr. ±21·1	1·97 ±0·32	20 Oct. ±17·9	0·44 ±0·08	1 Apr. ±18·4	8·04 ±0·48	16 Oct. ±5·9	0·39 ±0·10	7 Mar. ±19·8
Soay × Portland	7	47·1 ±8·2	11 Jul. ±3·1	5·1 ±0·6	18 Mar. ±5·6	2·11 ±0·19	27 Sept. ±6·8	0·45 ±0·04	31 Jan. ±23·4	7·05 ±1·03	25 Sept. ±3·5	0·61 ±0·04	27 Jan. ±2·0
Soay × Merino	4	45·5 ±5·7	12 Aug. ±9·8	7·1 ±0·5	25 Mar. ±10·8	1·33 ±0·23	22 Sept. ±11·3	0·47 ±0·52	15 Jan. ±3·6	5·78 ±0·50	30 Sept. ±0	0·53 ±0·06	7 Mar. ±8·4
Portland	5	182·7 ±25·5	30 Jun. ±8·9	46·3 ±3·7	19 Mar. ±11·9	2·01 ±0·14	30 Sept. ±13·9	0·84 ±0·12	3 Apr. ±13·9	6·58 ±0·16	22 Sept. ±3·2	0·22 ±0·04	15 Feb. ±5·1
Merino	7	34·0 ±5·6	29 Jun. ±3·9	6·9 ±0·9	19 Feb. ±10·6	0·69 ±0·09	24 Aug. ±17·4	0·30 ±0·04	4 Mar. ±11·4	2·57 ±0·23	31 Jul. ±16·3	0·53 ±0·06	5 Feb. ±17·0
Overall mean (individuals)	62	71·7 ±6·4	12 Aug. ±4·1	11·6 ±1·4	19 Mar. ±4·1	1·84 ±0·09	2 Oct. ±6·5	0·50 ±0·03	6 Mar. ±7·0	6·58 ±0·32	5 Oct. ±4·3	0·43 ±0·03	25 Feb. ±4·1
Overall mean (breeds)	11	72·9 ±12·8	14 Aug. ±8·8	12·0 ±3·5	20 Mar. ±5·0	11·83 ±0·09	8 Oct. ±7·9	0·50 ±0·06	5 Mar. ±11·6	6·69 ±0·54	6 Oct. ±7·5	0·42 ±0·04	26 Feb. ±5·5
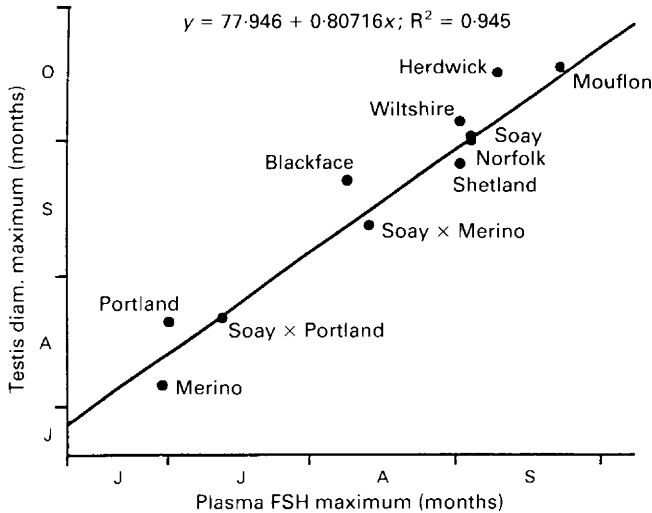
Fig. 3. Correlation between the time of the seasonal maximum in the blood plasma concentration of FSH and the seasonal maximum in the diameter of the testis for 11 breeds of sheep. Note the very close relationship between these two parameters since the peak in the plasma concentration of FSH precedes the peak in diameter of the testis by about 1 month in all breeds. Merino and Portland rams (southern types) have the earliest and mouflon rams (wild type) have the latest testicular cycle.

months later. The seasonal decline in the plasma concentration of FSH began in October at the time of maximum testicular activity, and the major regression of the reproductive axis occurred from November to March. These temporal changes resulted in a significant positive correlation between the seasonal changes in the plasma concentrations of FSH, inhibin and testosterone during the developing phase of the testicular cycle in summer (June–August, $r = 0.78$–0.92, $P < 0.01$) and during the regressing phase in winter (December–February, $r = 0.78$–0.94, $P < 0.01$) but not consistently at other times.

Annual cycle: comparison between breeds

The seasonal changes in the reproductive parameters in the mouflon, Herdwick and Merino rams are illustrated in Fig. 2 and the data for all breeds are summarized in Table 1. There were significant differences ($P < 0.001$, ANOVA) between breeds in the timing of the seasonal maximum in the plasma concentrations of FSH, inhibin and testosterone but not in the timing of the seasonal minimum for these parameters. There were also significant differences ($P < 0.01$, ANOVA) between breeds in the hormone concentration at the time of the seasonal maximum. The Merino was notable in showing the earliest seasonal peak with a relatively poorly defined annual reproductive cycle. The many differences between breeds can be deduced from the mean ± s.e.m. values presented in Table 1.

The difference between the breeds in the timing of the reproductive cycle is well illustrated by comparing the time of the seasonal maximum in the plasma concentration of FSH and the time of the seasonal maximum in diameter of the testis (Table 1; Fig. 3). There was a significant positive correlation between these two parameters ($R = 0.95$, $P < 0.001$), with the mouflon at one extreme (late reproductive cycle) and the Merino at the other (early reproductive cycle). There was also a significant between-breed correlation between the seasonal peak in plasma FSH and testosterone ($R = 0.65$, $P < 0.05$) but not for plasma FSH and inhibin ($R = 0.33$, NS).
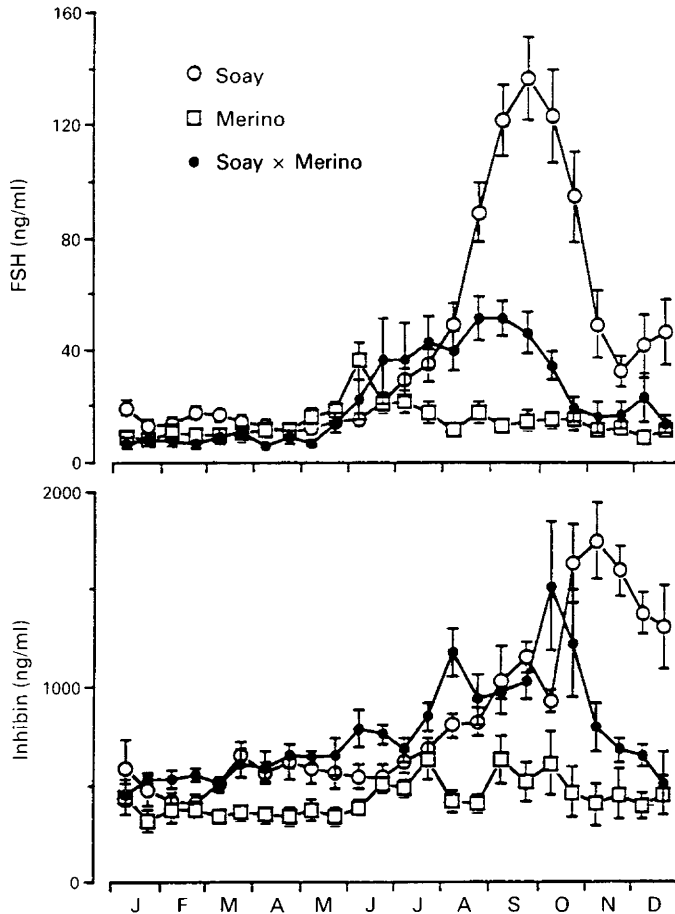
Fig. 4. Seasonal changes in the blood plasma concentration of FSH and inhibin in Soay ($\bigcirc$), Soay × Merino ($\bullet$) and Merino rams ($\square$). The values are mean $\pm$ s.e.m., $n = 4$–7 based on blood samples collected every half calendar month from about 9 months to 1 year 9 months old. The Soay × Merino were produced by mating a Merino ram with a group of Soay ewes.

Annual cycle: crossbred rams

The seasonal changes in the plasma concentrations of FSH and inhibin in the Soay, Merino and the Soay × Merino are illustrated in Fig. 4 and the data for all the parameters for the crossbred rams are summarized in Table 1. In both the Soay × Merino and the Soay × Portland, the magnitude and timing of the seasonal reproductive changes were intermediate between the pattern characteristic of the parents (Fig. 4). This was also evident from the relationship between the time of the seasonal maximum in plasma FSH and testicular diameter (Fig. 3). The physical appearance of the Soay × Merino and some of the other breeds used in the study is illustrated in Fig. 5.

Discussion

This study compares the seasonal reproductive physiology of wild, feral and domesticated sheep by monitoring endocrine changes in rams living under similar conditions at the same latitude. In all breeds of sheep there were seasonal changes in the circulating concentrations of FSH, inhibin and testosterone, associated with the seasonal testicular cycle. There were differences between the
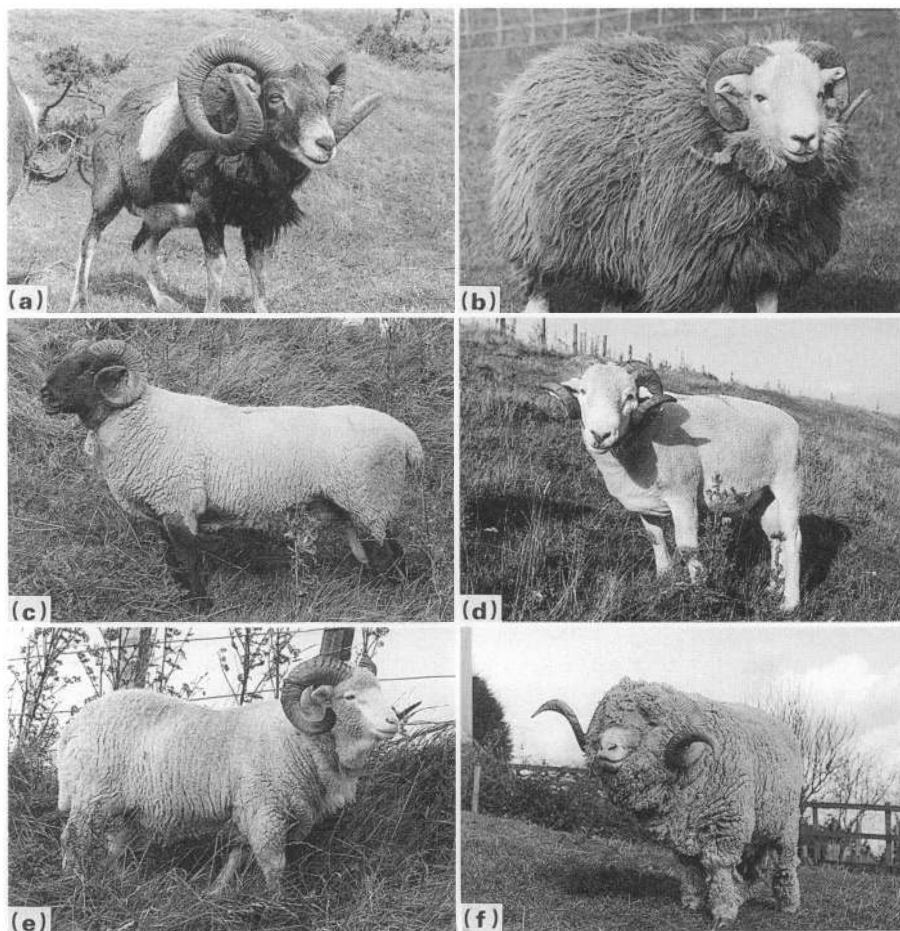
Fig. 5. Photographs of rams illustrating the clear morphological differences between breeds used in the current study: (a) mouflon; (b) Herdwick; (c) Norfolk; (d) Wiltshire; (e) Soay × Merino; (f) Merino.

breeds in both the magnitude and timing of the seasonal changes. The wild sheep (mouflon) showed a very clearly defined seasonal pattern in pituitary–testicular activity with the peak in testicular size occurring in October when the animals were showing overt rutting behaviour. The feral sheep (Soay) and most of the domesticated sheep showed a similar cycle but the seasonal changes were usually less marked and the peak in testicular size occurred about 1 month earlier. This trend was most evident in the two southern breeds (Portland and Merino) which showed maximum testicular activity as early as August. The crossbred rams, produced by mating Soay ewes with rams of the southern breeds, had a seasonal reproductive cycle intermediate in timing between the characteristic of the parents, demonstrating the genetic basis for the differences between breeds.

In the female, the transition from the anoestrous to the breeding season also varies between breeds, with the southern breeds showing an early and prolonged mating season (Hafez, 1952). While data are not available on the females of all the breeds included in this study kept at the same location, it is known that Merino ewes living near Edinburgh begin normal ovarian cycles in summer (July) at least 3 months in advance of the more seasonal breeds such as the Soay and the Boreray Blackface (Wheeler, 1973; Lincoln & Short, 1980). Since the rams of these breeds show similar differences in the timing of the testicular cycle, it is evident that the genetic mechanisms

determining the breed differences for the onset of the mating season apply to both sexes. The differences between the domesticated breeds and the wild type must represent the consequences of genetic selection for an earlier onset of fertility, thus allowing a longer lambing season; this is favoured if the animals are kept under a less seasonal environment, or if food is provided artificially to ensure survival of the lambs, as occurs in most domesticated flocks of sheep. The relationship between the timing of the mating season and the seasonality of the environment is also illustrated by the breeding patterns in the different species of wild sheep; the species living in the far north or at high altitudes have a late rut (Sadleir, 1969; Brunnel, 1982; Thomson & Turner, 1982).

In the current study, the clear differences between breeds in the time of the maximum testicular size was closely correlated with the time of the seasonal maximum in the blood plasma concentration of FSH. This indicates that the differences between breeds are primarily dictated by the seasonal pattern in the secretion of the gonadotrophic hormones from the anterior pituitary gland. Both FSH and LH (luteinizing hormone) are required for full testicular function in the ram (Courot, 1984; Haynes & Schanbacher, 1983; Lincoln, 1988). FSH controls the functional activity of the Sertoli cells to regulate spermatogenesis, and the parallel increase in the blood concentrations of FSH and inhibin during seasonal testicular redevelopment is consistent with the role of FSH in the control of inhibin secretion from the Sertoli cells (de Jong, 1987). This results in a positive correlation between the concentration of FSH and inhibin during the developing and regressing phases of the testicular cycle and a negative correlation during the active phase of the cycle (Lincoln & McNeilly, 1989). LH controls the secretory activity of the Leydig cells in the interstitial tissue of the testis, and the increase in blood concentrations of testosterone during testicular redevelopment reflects the role of LH in regulating steroidogenesis. Since the secretion of both FSH and LH is dictated by the release of GnRH (gonadotrophin-releasing hormone) from the hypothalamus (Lincoln, D. W. *et al.*, 1985; Clarke, 1988), it follows that the seasonal reactivation of the reproductive axis is governed by the hypothalamus, and differences between breeds in the timing of the testicular cycle reflect differences in the endocrine regulation by the hypothalamus.

In sheep, the mechanisms operating in the brain to regulate the seasonal testicular cycle are too poorly understood to provide a full explanation for the breed variation in reproduction. Experimental studies indicate that long-term cycles in testicular activity and other seasonal characteristics can be generated endogenously, but under outdoor conditions this cycle is amplified and entrained by the influence of environmental cues (Lincoln & Davidson, 1977; Howles *et al.*, 1982; Lincoln *et al.*, 1989). These cues include the seasonal change in daylength, temperature and nutrition which are most conspicuous at higher latitudes. Differences in one or more of the neuronal components which generate the endogenous long-term rhythm or which relay the influences of the environment may account for the variation in reproductive physiology between breeds.

There is evidence that the response to changes in daylength varies between breeds, with the more seasonal northern breeds such as the Finnish Landrace, Suffolk and Romney Marsh, showing a greater stimulated response in pulsatile LH secretion and testicular activity following exposure to a change from long days to short days compared to the less seasonal breeds such as the Dorset, Rambuillet and Merino (D'Occhio *et al.*, 1984; Evans & Robinson, 1980; Poulton & Robinson, 1987). A corollary of this is that the less seasonal breeds retain a higher level of pulsatile LH secretion and sexual behaviour during long days (Bremner *et al.*, 1980; Poulton & Robinson, 1987). Since the pineal gland relays the effects of daylength through the temporal pattern of melatonin secretion, breed differences might be expected in this component of the photoperiodic relay. However, measurements of the 24-h profiles in the concentrations of melatonin in breeds which differ in the seasonality of reproduction have shown the duration of the period of increased melatonin secretion reflects the period of darkness under natural photoperiods, with no obvious difference between breeds (e.g. Merino: Kennaway *et al.*, 1982; Finn × Dorset/Rambouillet: Kennaway *et al.*, 1983; Ile de France: Ravault & Thimonier, 1988; Suffolk: Schanbacher, 1988; Soay: Lincoln, G. A. *et al.*, 1985). This indicates that it is not the melatonin signal which differs between breeds but the way the signal is translated in the brain.

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In the highly seasonal breeds of sheep such as the Soay, the importance of the response to daylength is apparently to delay the onset of the mating season. This has been demonstrated in a study in which the photoperiodic response in Soay rams has been blocked by pinealectomy and the animals have been kept outside with normal rams as in the current study (Lincoln *et al.*, 1989). Under these conditions, pinealectomized Soay rams show an attenuated seasonal testicular cycle with maximum testicular size in summer some 2 months earlier than in the control rams. In these experimental animals, the seasonal cycle in testicular activity runs in close parallel with the seasonal changes in the quality of the diet which is maximum in summer. This indicates that the response to daylength in the normal animal overrides or modifies the response to nutrition to influence the seasonal reproductive cycle. This results in a greater suppression of pituitary–testicular activity during long days in spring and summer, and thus a longer latency to the peak in testicular activity in the autumn. The seasonality in the pinealectomized Soay rams appears analogous to that occurring in the southern breeds of sheep, including the Merino and Portland, which also show an early seasonal maximum in testicular activity in summer and which are relatively unresponsive to daylength. Differences between breeds in the response to daylength may therefore be of major importance in determining the differences in the timing of the testicular cycle described in the current study.

In conclusion, this study compares for the first time the reproductive seasonality of wild, feral and domesticated breeds of sheep kept at one locality. The most consistent difference between the wild-type and the other breeds was in the time of the seasonal maximum in the circulating concentration of FSH and the size of the testis. In the wild-type sheep the seasonal peak in testicular activity was in September and October, in the domesticated breeds it was earlier in the year, especially in the most southern breeds, and in the cross-breeds the pattern was intermediate. The results are consistent with the role of FSH in the stimulation of testicular growth and the secretion of inhibin during the seasonal reactivation of the testicular axis. The differences between breeds may be explained by differences in the central neuroendocrine mechanisms relaying the effects of daylength and controlling the secretion of gonadotrophic hormones from the pituitary gland.

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