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Seasonal effects on birth weight in sheep are associated with changes in placental development

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Seasonal effects on birth weight in sheep are associated with changes in placental development

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Abstract Lambs born in the autumn or winter have substantially lower birth weights than those born in the spring, but the physiological basis of this difference is unknown. This study examined the effects of season on foetal growth and placental development in ewes managed under controlled grazing to minimise the confounding effects of maternal liveweight change. Mature Romney ewes pregnant to matings in December ($n = 13$) or March ($n = 13$), with similar liveweights at mating, were managed to achieve similar liveweights at Day 140 of gestation. At that time, measures of foetal growth and placental development, adjusted for litter size, were (December- versus March-mated): foetal weight (4.15 ± 0.16 versus 5.07 ± 0.16 kg, $P < 0.001$); total foetal weight per ewe (6.42 ± 0.18 versus 7.14 ± 0.22 kg, $P < 0.01$); caruncle number (114.5 ± 4.1 versus 121.0 ± 4.2, $P > 0.10$); placentome number (89.4 ± 4.2 versus 106.9 ± 4.3, $P < 0.01$); number of placentomes per number of caruncles (0.79 ± 0.03 versus 0.88 ± 0.03, $P < 0.05$); and total placentome weight (564.7 ± 34.0 versus 679.0 ± 34.9 g, $P < 0.05$). Maternal circulating concentrations of prolactin, IGF–1, and growth hormone are reported. This study has demonstrated that the marked seasonal differences in foetal growth are associated with seasonal differences in placental size, the formation of placentomes being significantly reduced in December-mated ewes.

Keywords season; birth weight; placental development; foetal growth; prolactin; sheep

INTRODUCTION

In New Zealand, lambs born in the autumn or winter have lower birth weights than spring-born lambs by 0.4–1.0 kg (Reid et al. 1988; Peterson 1992; Morris et al. 1993). Given that lamb birth weight has an important effect on the survival and growth of lambs (Schinckel & Short 1961; McCutcheon et al. 1981), this is an important finding for sheep production. The seasonal effect on birth weight cannot be accounted for entirely by differences in maternal nutrition and may be a consequence of other seasonally related factors such as photoperiod or ambient temperature, mediated perhaps by effects on placental function or on the growth capacity of the foetus.

Seasonal changes in reproductive activity, food intake, and growth are strongly influenced by changes in photoperiod, and are associated with large alterations in the secretion of pituitary hormones such as prolactin (Ravault & Ortavant 1977) and growth hormone (Barenton et al. 1988). There could also be transfer of photoperiodic information to the foetus, via the placenta, as occurs in the hamster (Weaver & Reppert 1986), but the neuroendocrine mechanisms responsible for the control of prolactin secretion from the foetal sheep pituitary gland are not functional until Day 100 of gestation (Bassett et al. 1989). Exposure of ewes to a long-day photoperiod during the last 6 weeks of a winter gestation significantly increased maternal plasma prolactin concentrations to levels similar to those observed during summer pregnancies (Bassett et al. 1988). Corresponding increases in circulating prolactin concentrations occurred in the lambs at birth, but there was no effect of the 6-week photoperiod treatment on lamb birth weight (Bassett

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1992). This latter finding contrasts with the observations of Bocquier (1985) who reported that ewes subjected to a long-day photoperiod from Day 100 of gestation produced heavier twin lambs than similar ewes maintained under short days, even though food intake of the two groups was identical. However, neither study involved manipulation of photoperiod during early gestation.

The objective of this study was to determine whether seasonal differences in foetal growth, and hence in birth weight, are associated with differences in placental development and circulating maternal hormone concentrations, in situations where differences in maternal liveweight change are minimised.

MATERIALS AND METHODS

Animals and treatment

The trial was conducted at Massey University's Haurongo Research Unit (latitude 40.23°S and longitude 175.37° E). The study involved 26 Romney ewes aged 5 and 6 years which were pregnant to December (n = 13) or March (n = 13) mating. All ewes had lambed in the previous August/September (spring) and were randomly allocated to treatment groups after their lambs were weaned in mid November. Both groups of ewes were shorn 1 month before mating.

Mating in December (rams joined 21 December) was accomplished using a combination of progesterone-impregnated controlled internal drug releasers (Eazi-breed CIDR Type G, Carter Holt Harvey Plastic Products, Hamilton, New Zealand) and pregnant mare serum gonadotrophin (PMSG Folligon, Intervet International B. V. Boxmeer, Holland) to induce ovulation outside the normal breeding season, and high ram to ewe ratios. The CIDRs were inserted for 14 days. PMSG (400 i.u./ewe) was injected intramuscularly the day before CIDR removal. March mating of ewes (rams joined 22 March) was as above, but PMSG was not used. Four mature Border Leicester × Poll Dorset rams were introduced at CIDR withdrawal, the same four rams being used in December and March.

Rams were harnessed with sire-sine mating crayons, and crayon marks were recorded on a daily basis (between 1600 and 1800 h). Single or multiple pregnancy was assessed at Days 58 and 70 of pregnancy using real-time ultrasound scanning. All ewes in the trial were pregnant to matings in the first 72 h after CIDR removal.

Ewes in each group were managed as two separate mobs on pasture, mainly ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), to achieve similar patterns of liveweight change from mating to slaughter. Ewes were weighed off pasture (between 0900 and 1100 h) every 2 weeks. Grazing was controlled using electric fences from late December until early February to maintain ewes to be mated in March at the 55.6 kg mating weight of December-mated ewes.

Ewes were blood-sampled by jugular venipuncture at 0800 h on Days 70 and 100, and immediately before slaughter on Day 140 of gestation to determine circulating concentrations of prolactin, growth hormone (GH), and insulin-like growth factor–1 (IGF–1). Samples (8 ml) were withdrawn into vacutainers (Becton Dickinson Vacutainer Systems, Rutherford, New Jersey 07070) containing EDTA as the anticoagulant and immediately placed on ice. Within 1 h the samples were centrifuged at 3000 g and 4°C for 20 min. Plasma was pipetted into triplicate vials and stored at –20°C until assayed.

Measurements

Dimensions of the mammary gland of each ewe were measured in duplicate on Day 139 of gestation (the day before slaughter) as described by Mellor & Murray (1985).

Ewes were slaughtered immediately off pasture, commencing at 0830 h on Day 140 of gestation, by stunning with a captive bolt pistol and exsanguination. The mammary gland was dissected off, trimmed of skin, fat, and connective tissue, and weighed. The abdominal cavity was opened and the uterus removed. A ligature was tied at the junction of the cervix and uterus, and the cervix, vagina, and associated tissue were removed. The whole gravid uterus was then weighed. The allantoic and amniotic fluids were removed separately and weighed. The foetus(es) were removed from the uterus and the umbilical cord ligated at the abdomen before being cut. Foetal number, weight, and sex were recorded. Foetal crown-rump length was measured (Mellor & Matheson 1979). Foetal liver, spleen, heart, kidneys, lungs, brain, thyroid, and thymus were removed, blotted dry, and weighed (combined weights of bilateral organs). Placentomes were dissected from the uterus, separated into their maternal (caruncle) and foetal (cotyledon) components, counted, and their individual weights recorded. The myoendometrium was then weighed.

The liver, spleen, heart, kidneys, lungs, and thyroid of the ewes were removed, blotted dry, and weighed (combined weights of bilateral organs). The reticulo-rumen, omasum, abomasum, small intestine, and caecum were also removed, flushed of their contents, blotted dry, and weighed. Carcasses were weighed hot.

Assays

Plasma glucose concentration was determined using a Cobas Fara II autoanalyser (Roche Products, Basel, Switzerland) based on the enzymatic colourimetric method of Bergmeyer (1974). Intra- and inter-assay coefficients of variation were 1.6 and 2.3%, respectively.

Plasma IGF–1 concentration was measured by radioimmunoassay (RIA) using a rabbit antiserum to recombinant human IGF–1 (878/4) at a final titre of 1:250 000 (Breier et al. 1991a). The antiserum has a cross-reaction with IGF–2 of less than 0.05%, a minimum detectable dose of 0.06 ng/tube, and a half displacement dose of 0.03 ng/tube. Before RIA, plasma samples were subjected to acid-ethanol extraction with an additional cryoprecipitation step. This extraction and assay have been extensively validated for ovine plasma (Breier et al. 1991a). Using this method, the intra- and inter-assay coefficients of variation for IGF–1 were 5.0 and 9.8%, respectively. IGF–1 concentrations are expressed in terms of the international reference recombinant human IGF–1 preparation 87/518 (National Institute for Biological Standards and Control, Potters Bar, Herts, U.K.).

Growth hormone (GH) concentration was measured using the heterologous double antibody RIA described by Flux et al. (1984). The GH assay used bovine GH for iodination (USDA–bGH–I–1, 3.2 i.u./mg) and reference standards (USDA–bGH–B–1, 1.9 i.u./mg). Intra- and inter-assay coefficients of variation for GH were 8.6 and 13.2%, respectively.

The prolactin assay was a homologous double-antibody competitive binding RIA based upon the method of van Landeghem & van de Wiel (1978). The first antibody, NIADDK-anti-oPRL–1 (AFP–973269) rabbit anti-ovine prolactin antiserum, donated by NIADDK and supplied through the National Hormone and Pituitary Program, University of Maryland School of Medicine, was used at a working dilution of 1:50 000 (final dilution 1:550 000). The second antibody, donkey anti-rabbit IgG (Lot No. 20796, IDS, Washington, Tyne and Wear, England) was used at a working dilution of 1:40. Assay binding was typically 45–55% and assay sensitivity about 1 μg/l. Three ovine plasma samples, assayed neat or at stepwise serial dilutions up to final dilutions of 1:128, 1:256, and 1:512, exhibited parallelism with the standards. Plasma samples were assayed in triplicate. The mean intra-assay coefficient of variation (CV) calculated over 12 assays was 7.5% and the mean inter-assay CV was 14.5% for three reference plasma samples corresponding with the linear portion of the standard curve.

Statistical methods

Analysis of covariance was used to test effects of season on weights of maternal organs and uterine components (adjusted to a common maternal liveweight and pregnancy rank (single versus multiple)) and on foetal weight and foetal organ weights (adjusted for foetal weight, rank, and sex). Univariate and multivariate (repeated measures) analyses of variance were used to analyse differences in hormone and metabolite concentrations in the ewes. Data are expressed as least square means and standard errors for the two groups of ewes and their foetuses. Statistical analyses were conducted using the computer package 'REG' (Gilmour 1990).

Preliminary results of this study were reported by Jenkinson et al. (1994).

RESULTS

Ewes mated in December versus March had a similar liveweight at mating (55.6 ± 1.8 versus 55.7 ± 1.9 kg, $P > 0.10$) and at slaughter (62.5 ± 1.8 versus 62.9 ± 1.9 kg, $P > 0.10$). The maximum difference in liveweight between the two groups (59.0 ± 2.0 versus 54.9 ± 2.0 kg, $P > 0.10$) occurred at Day 70. As a result, there was a significant ($P < 0.001$) difference in maternal liveweight gain from Day 70 to Day 140 of gestation (3.5 ± 1.0 versus 8.0 ± 0.6 kg).

The 13 ewes pregnant to the December mating carried nine singles, two sets of twins, and two sets of triplets, whereas the 13 ewes pregnant to the March mating carried eight singles and five sets of twins.

Table 1 shows the liveweights, carcass weights, dressing-out percentages, organ weights, and alimentary canal segment weights of the December- and March-mated ewes. Weight of the abomasum was the only one of these significantly affected by

season, being greater ($P < 0.01$) in December- than in March-mated ewes.

Foetuses from the March-mated ewes had higher ($P < 0.001$) mean body weights (5.07 ± 0.16 kg) than foetuses from the December-mated ewes (4.15 ± 0.16 kg, Table 2). Thymus weights were significantly ($P < 0.001$) higher in foetuses from December-mated ewes but thyroid weights were higher ($P < 0.05$) in foetuses from March-mated ewes. Crown-rump length and weights of other foetal organs were not significantly different between lambs conceived in the two seasons.

Mammary gland dimension was not different between ewes mated in the two seasons but mammary gland weight was significantly ($P < 0.05$) higher in the March-mated ewes (Table 3). Total foetal weight per ewe was higher ($P < 0.01$) in the March-mated ewes, as was total weight of the gravid uterus ($P < 0.05$), although there were no significant differences between seasons in weight of the myoendometrium or foetal fluids. March-mated ewes had a significantly ($P < 0.01$) greater number of placentomes formed and, since there was no difference in weight of individual

Table 1 Effect of season on final liveweight, carcass weight, dressing-out percentage, organ weights, and alimentary canal segment weights in December- and March-mated ewes at Day 140 of gestation (Mean ± SE).

	December-mated	March-mated
n	13	13
Final liveweight (kg)	62.5 ± 1.8	62.9 ± 1.9
Carcass weight (kg)	23.3 ± 0.7	23.5 ± 0.7
Dressing-out (%)	37.5 ± 1.2	37.2 ± 1.2
Organ weight (g)		
Liver	887.5 ± 24.4	856.1 ± 24.6
Lungs	508.5 ± 11.5	502.0 ± 12.0
Heart	255.9 ± 6.4	254.0 ± 4.6
Spleen	82.0 ± 8.1	96.5 ± 8.4
Kidneys	137.4 ± 3.4	147.5 ± 3.6
Thyroid	5.64 ± 0.48	5.68 ± 0.50
Alimentary canal segment (g)		
Reticulo-rumen	950.5 ± 19.5	935.7 ± 20.3
Omasum	99.9 ± 5.0	110.8 ± 5.2
Abomasum	430.8 ± 19.6	341.0 ± 20.4**
Small intestine	1073.8 ± 43.5	1051.2 ± 45.3
Caecum	85.1 ± 4.7	83.3 ± 4.9

**$P < 0.01$

Table 2 Crown-rump length, body weight, and organ weights of foetuses from December- and March-mated ewes at Day 140 of gestation (Mean ± SE).

	December-mated	March-mated
n	19	18
Crown-rump length (cm)	56.0 ± 0.4	56.8 ± 0.4
Weight (g)		
Body	4154.5 ± 156.6	5074.3 ± 161.3***
Brain	47.33 ± 2.01	51.33 ± 2.07
Liver	92.07 ± 2.62	97.37 ± 2.70
Lungs	117.90 ± 3.14	122.96 ± 3.24
Heart	31.84 ± 0.69	32.13 ± 0.71
Spleen	5.27 ± 0.18	5.15 ± 0.17
Kidneys	22.36 ± 0.71	22.73 ± 0.73
Thyroid	1.85 ± 0.18	2.56 ± 0.18*
Thymus	19.05 ± 0.92	13.87 ± 0.95***

*$P < 0.05$; ***$P < 0.001$

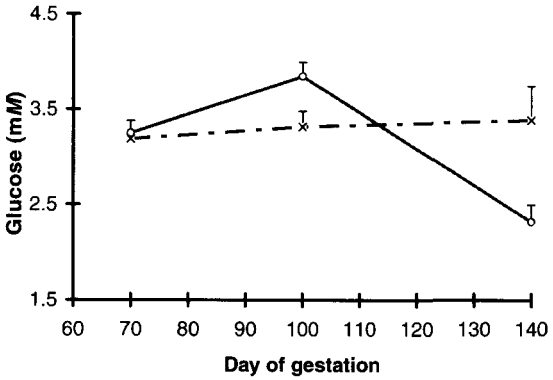

Fig. 1 Maternal circulating concentrations of glucose from Day 70 to 140 of gestation in ewes mated in December (- - -x- - -) or March (—o—). Vertical bars represent the standard error of the mean.

placentomes, a greater total placentome weight ($P < 0.05$). The numbers of caruncles in December- and March-mated ewes were similar but caruncle occupancy (i.e. number of placentomes per number of caruncles) was greater ($P < 0.05$) in the March-mated ewes (Table 3).

Maternal glucose concentrations remained stable throughout mid–late gestation in the December-mated ewes, but declined sharply after Day 100 of gestation in the March-mated ewes (Fig. 1). Glucose concentrations did not differ significantly at Days 70 or 100 of gestation but were significantly ($P < 0.001$) higher in December-mated ewes at Day 140 of gestation.

Maternal plasma prolactin concentrations (Fig. 2) were higher in December-mated ewes at Day 70 of gestation ($P < 0.001$) and in March-mated ewes at Day 100 of gestation ($P < 0.001$), but did not differ significantly between December- and March-mated ewes at Day 140 of gestation. There was a significant ($P < 0.001$) stage of gestation by season interaction.

In both December- and March-mated ewes, circulating growth hormone concentrations remained stable from Days 70 to 100 of gestation, then began to increase steadily up until Day 140 of gestation, at which time the ewes were slaughtered. There were no significant differences in growth hormone concentrations from Days 70 to 140 of gestation.

There was a significant ($P < 0.001$) season by stage of gestation interaction for circulating maternal IGF–1 concentrations, reflecting the fact that IGF–1 concentrations in the December- and March-mated ewes diverged during late gestation. Although circulating concentrations of IGF–1 were significantly ($P < 0.05$) higher in the December-mated ewes at Day 70, they were significantly ($P < 0.001$) lower at Day 140 of gestation.

Table 3 Effect of season on mammary gland dimension and weight, and uterine components in December- and March-mated ewes at Day 140 of gestation (Mean ± SE).

	December-mated	March-mated
n	13	13
Mammary gland dimension (mm)	476.9 ± 22.0	465.2 ± 26.1
Weight (g)		
Mammary gland	297.7 ± 28.6	383.0 ± 33.7*
Gravid uterus	10453.7 ±302.9	11373.1 ±358.9*
Total foetal weight	6417.3 ±183.8	7139.3 ±215.1**
Amniotic fluid	1362.2 ±121.3	1191.7 ±143.8
Allantoic fluid	1037.5 ±103.0	930.7 ±122.1
Myoendometrium	632.3 ± 21.8	672.2 ± 22.4
Caruncle (individual)	1.09 ± 0.10	1.37 ± 0.12*
Cotyledon (individual)	5.01 ± 0.38	4.78 ± 0.39
Placentome (individual)	6.31 ± 0.41	6.28 ± 0.43
Placentomes (total)	564.7 ± 34.0	679.0 ± 34.9*
Total foetal / Total placentome	11.5 ± 0.7	10.4 ± 0.8
No. of caruncles	114.5 ± 4.1	121.0 ± 4.2
No. of placentomes	89.4 ± 4.2	106.9 ± 4.3**
Caruncle occupancy[a]	0.79 ± 0.03	0.88 ± 0.03*

[a]Number of placentomes/number of caruncles; *$P < 0.05$; **$P < 0.01$

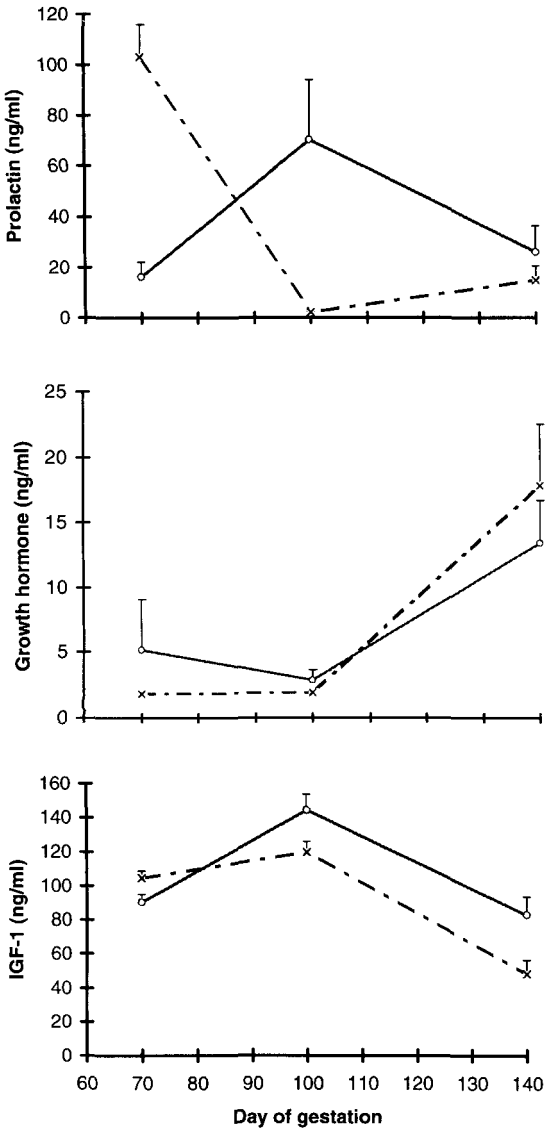

Fig. 2 Maternal circulating concentrations of prolactin, growth hormone and IGF–1 from Day 70 to 140 of gestation in ewes mated in December (- – -×- – -) or March (—○—). Vertical bars represent the standard error of the mean.

DISCUSSION

The effect of season on foetal weight at Day 140 of gestation (and by inference on birth weight) observed in this study is consistent with the findings of Reid et al. (1988), Peterson (1992), and Morris et al. (1993). However, our results suggest that the effect is not due solely to differences in maternal nutrition as measured by changes in ewe bodyweight. Rather, there appears to be an effect of season on placental development and specifically on the number of placentomes formed.

Both groups of ewes followed a similar pattern of liveweight change as pregnancy progressed, except at Day 70 of gestation when a non-significant difference in liveweight of 4.1 kg (6.9%) occurred between the two groups (the group with the lowest liveweight at this point eventually having the heaviest lambs). Much larger differences in absolute liveweight (10–12 kg) have been generated in 50 kg grazing ewes up to Day 100 of gestation without any significant carry-over effects on lamb birth weight, provided that the level of feeding is adequate in late pregnancy (Parr et al. 1986; Rattray et al. 1987). August-lambing ewes produced heavier lambs at birth than June-lambing ewes, even when pasture was allocated on the basis of residual herbage mass (kg DM/ha) with the same targets set for each lambing group (Morris et al. 1993). Reid et al. (1988) recorded much smaller changes in liveweight from joining to lambing in spring-lambing ewes compared to autumn-lambing ewes, but still observed differences in birth weight of 0.4 kg (in favour of the spring-lambing ewes) across two consecutive seasons. In the present study, ewes did not differ in final liveweight, carcass weight, dressing-out percentage, or organ weights, (with the exception of abomasal weight which was lowest in the group of ewes (March-mated) with the highest foetal weights). The difference in maternal liveweight gain from Day 70 to 140 could, however, have contributed to the difference in foetal growth. It is unlikely that the difference in foetal weight reflects the different time from weaning to mating in the two groups of ewes. Morris et al. (1993) found similar seasonal effects on birth weight in ewes which lambed in the two seasons over three consecutive lambings and which, at the last two of these lambings, had similar weaning to mating intervals.

The reduced total and average foetal weight (adjusted for litter size) in December-mated compared to March-mated ewes was associated with a reduced number of placentomes and reduced total placental weight. This was in turn the result of a lower occupancy of maternal caruncles by fetal cotyledons, despite the total number of available caruncles being similar in December- and March-mated ewes. Experimental reduction in placental size (e.g., by caruncletomy or placental ablation) has also been shown to reduce foetal

weight and dimensions, with birth weight tending to decline as the number of caruncles removed increases (Alexander 1964b; Mellor et al. 1977; Owens et al. 1987). In the present study, the ratio of total foetal weight to total placental weight was not different between the two groups of ewes, suggesting that the impaired foetal growth in lambs conceived in December was causally related to their lower placental weights.

The number of placentomes associated with each foetus is supposedly fixed at implantation, but the total weight of placentomes increases until about 90 days of gestation after which there is little change (Alexander 1964a). This would suggest that the seasonal effect on placentome number observed here arose at the time of implantation in each group of ewes and was not caused by differences in maternal liveweight gain in the second half of gestation. However, there is some evidence that endocrine changes in mid–late pregnancy can influence placentome number. Recent investigations (S. H. Min, unpubl. data) have shown that treatment of pregnant ewes with bovine growth hormone for a period of only 10 days beginning at Day 100 of gestation tended to increase the number of placentomes. This supports the observation of Stelwagen et al. (1994) that the treatment of ewes with growth hormone for a period of 28 days increases the placentome number. However, both studies failed to demonstrate an increase in either total placental weight or foetal weight. In addition, these investigations were of short duration and involved manipulations in the last third of gestation. Thus while the possibility exists that the seasonal difference in placentome number/weight, and hence in foetal growth, observed in the present study arose in later pregnancy rather than at implantation, an implantation effect seems more likely. However, because the ewes were slaughtered only at Day 140 of gestation, precise timing of the seasonal effect on placental size cannot be determined.

Growth hormone is an important regulator of postnatal growth (Spencer 1985), but does not appear to play a significant role in the regulation of foetal growth (Gluckman 1984). Differences in growth hormone concentration between the two groups of ewes were not significant and were much smaller than those in previous studies in which growth hormone treatment of ewes led to differences in placental development. They are thus unlikely to explain the seasonal differences in foetal and placental development.

Changes in maternal plasma insulin-like growth factor–1 (IGF–1) concentrations (between December- and March-mated ewes and during pregnancy) were the reverse of those in growth hormone. Thus the decline in IGF–1 in late gestation may reflect growth hormone resistance (i.e. down-regulation of hepatic growth hormone receptors associated with nutritional stress; Breier et al. 1991b). The difference in maternal IGF–1 concentrations observed between the groups from Day 100 to 140 of gestation was small compared to that associated with improved foetal growth in rodents (Gluckman et al. 1992) and thus is unlikely to have contributed to the seasonal effect. Differences in maternal circulating glucose concentrations (especially at Day 140) most likely reflect greater foetal drain in the March-mated ewes (Mellor & Murray 1982) and thus are likely to be an effect, rather than a cause, of the differences in foetal growth rate.

The marked seasonal differences in foetal and placental development were associated with differences in maternal circulating concentrations of prolactin. In December-mated ewes, prolactin concentrations were high at Day 70 of gestation (2 March) and declined markedly to Day 100 (1 April), remaining low until Day 140 (11 May). In the March-mated ewes, concentrations of prolactin were low at Day 70 (31 May, and similar to those in December-mated ewes at approximately the same actual time), rose to Day 100 (30 June), mainly because three single-bearing ewes had very high plasma prolactin concentrations, and then declined to Day 140 (10 August). In general, therefore, the patterns of maternal plasma prolactin concentrations were consistent with previous reports (Ortavant et al. 1988; Peterson et al. 1990), i.e. elevated concentrations in summer, declining through the autumn to low values in winter. It is not possible to determine whether these changes were causally related to seasonal differences in placental/foetal development, partly because the stage of gestation at which these differences arose could not be determined from the present study. However, it is tempting to speculate that the marked differences in maternal prolactin concentrations at Day 70 of gestation (and, by inference, earlier in pregnancy) between December- and March-mated ewes could be related to the differences in caruncle occupancy and placentome formation, differences which (as noted earlier) are most likely to have arisen around the time of implantation.

The December-mated ewes had lower (by about 22%) mammary gland weights than March-mated ewes but no difference in gland dimensions. Studies in the goat (Forsyth et al. 1985) have shown that suppression of maternal prolactin secretion can lead to some delay in mammary development. Furthermore, milk production was found to be significantly lower in ewes mated out-of-season (December) than in those mated in-season (March), the lower milk yields being associated with lower plasma prolactin concentrations (Peterson et al. 1990). The fact that December-mated ewes had lower gland weights but not dimensions than the March-mated ewes in the present study suggests a smaller pre-partum accumulation of secretion in the former group. Informal observation in the present study suggested that, at slaughter, mammary gland secretions were present in the March-mated ewes but not in the December-mated ewes. This is consistent with the results of Peterson et al. (1990) but the possibility also exists that there was a seasonal effect on growth of mammary tissue per se, possibly as a consequence of differential secretion of placental hormones.

In conclusion, this study has demonstrated that the marked differences in foetal growth observed between December- and March-mated ewes are associated with, and likely to be the result of, corresponding differences in placental development, specifically the formation of placentomes rather than growth of individual placentomes. This effect is most likely to occur in early gestation but its exact timing, and the mechanism by which season influences this process, remain to be determined.

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