Influence of Breed of Fetus on Periparturient Endocrine Responses and Subsequent Milk Production of Ayrshire Dams[1]

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ABSTRACT

Purebred Ayrshire females were assigned to two groups based on the breed of fetus carried during gestation. In group 1, Limousin embryos were transferred nonsurgically into Ayrshire recipients (10 heifers and 1 cow), and in group 2, 11 Ayrshire heifers and 1 cow were inseminated artificially to Ayrshire bulls. Blood samples were collected daily from d 265 of gestation until d 15 postpartum from 5 heifers of each group. Milk yield was recorded on alternate weeks during the first 20 wk postpartum. Calf birth weight was higher (44.2 vs. 35.4 kg) and gestation was longer (297.4 vs. 280.2 d) in Ayrshire dams bearing Limousin fetuses than in those bearing Ayrshire fetuses. Daily milk production for the first 20 wk was lower (18.1 vs. 20.8 kg) in Ayrshire dams bearing Limousin fetuses than in those bearing Ayrshire fetuses. Prepartum decrease in progesterone concentrations and increase in estrone concentrations were faster in Ayrshire heifers bearing Limousin fetuses than in those bearing Ayrshire fetuses. Profiles of peripartum concentrations of bovine placental lactogen differed between Ayrshire dams carrying different families of Limousin fetuses but were similar in those carrying families of Ayrshire fetuses. The concentrations of 15-keto-13,14-dihydroprostaglandin $F_{2\alpha}$ were lower during the postpartum period in heifers that gave birth to Limousin calves than in those that had Ayrshire calves. In conclusion, the breed of fetus influences physiological and endocrine responses of the dam, which might have some effect on milk production of the dam.
(Key words: fetal effects, milk production, endocrine responses)

INTRODUCTION

After embryo transfer, fetal and maternal units are genetically independent. Studies of large herd data set (16, 17) clearly indicated that gestation length, calf birth weight, and calving ease are affected by the donor breed. Moreover, experiments with mixed breed pregnancies in sheep indicated that fetal genotype controls the duration of pregnancy and regulates fetal production of steroids implicated in the process of parturition (18).

Pregnancy is the major stimulation for growth of the mammary gland and lactogenesis during the natural life cycle (26). Milk production of the dam as well as other production and reproduction traits such as calf birth weight, gestation length, calving ease, and days open are influenced by the service sire (1, 14, 22, 23). Sire of fetus effects are transmitted par-

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tially to the dam via the fetus she bears. Selection for milk yield influences various physiological, hormonal, and production responses of Jersey cows during the periparturient period (9). Furthermore, breed of service sire directly affects hormone concentrations of maternal (progesterone, 15-keto-13,14-dihydroprostaglandin $F_{2\alpha}$) and conceptus (estrogen) origins (12, 13) during the periparturient period in cattle.

Potential effects of breed of transferred embryos on production and endocrine response of the dam are unknown. The objective of this experiment was to determine the effect of breed of fetus on production and endocrine responses of Ayrshire dams during the periparturient period.

MATERIALS AND METHODS

Animals

Twenty-one purebred Ayrshire heifers and two primiparous Ayrshire cows from the same commercial dairy farm were used in this experiment. Animals were assigned to two groups based on the breed of fetus carried during gestation. In group 1, purebred Limousin embryos collected from three purebred Limousin dams inseminated by four purebred Limousin sires were transferred nonsurgically into purebred Ayrshire recipients (heifers, n = 10; cow, n = 1). Group 2, the control group, consisted of 11 Ayrshire heifers and 1 cow inseminated artificially to 6 purebred Ayrshire sires. Animals from each group calved contemporaneously during two periods lasting from June 28 to November 22, 1985 and from December 8, 1985 to January 28, 1986. The average age at calving was 30.3 ± 3.9 mo. Feeding and management were similar in both groups during the two calving periods.

At calving, calf birth weight, viability, and sex were recorded, and gestation length was calculated. Milk yield and fat content were recorded on alternate weeks during the first 20 wk postpartum.

Additionally, blood samples from the caudal vein or artery were collected daily into heparinized vacutainer tubes between d 265 of gestation and d 15 postpartum from the 10 heifers (5 per group) that calved during the second period. Plasma was harvested and stored at –20°C until subsequent analyses.

Hormone Analyses

All estimates of hormone concentrations were done in duplicate by radioimmunoassay procedures. Plasma concentrations of progesterone (10) and of estrone (see validation) during the prepartum period, of bovine placental lactogen (bPL; 3) from d –15 to 6 postpartum, and of 15-keto-13,14-dihydroprostaglandin $F_{2\alpha}$ (PGFM; 13) from d –3 to 15 postpartum were measured.

Estrone was extracted (plasma volume = .5 to 1.0 ml) and assayed by the method described previously for estradiol-17β (10), except that a specific antibody against estrone (no. 100A; 5) was used at a dilution of 1:50000. Recovery of added (X, 10 to 240 pg/tube) (X) versus measured ($\hat{Y}$) estrone concentrations was described by linear regression ($\hat{Y}$ = –3.54 + 1.1X; r = .99). Estrone concentrations did not differ ($P>.1$) between assays and were not influenced ($P>.1$) by assay volume. Sensitivity of the assay was 10 pg/tube. Serial dilutions of plasma samples collected from an ovariectomized cow and containing known amounts of estrone or of pooled plasma samples from cows in late pregnancy displayed inhibition curves that apparently were parallel (homogeneity of regression; $P>.1$) to the standard curve. Intraassay and interassay coefficients of variation were 11.2 and 8.7% for estrone, 10.4 and 8.5% for progesterone, 6.5 and 4.5% for PGFM, and 8.5 and 10.2% for bPL.

Statistical Analyses

Data were analyzed by least squares ANOVA using the general linear models procedures of SAS (24). For milk yield and composition, experimental design was a split plot in which animals were nested in groups (i.e., breed of fetus carried). Milk yield and composition data from the two periods were pooled for each group, as no group × period × time interaction was detected ($P>.1$).

The 10 Ayrshire heifers from which endocrine data were derived carried either two full-sibling combinations (i.e., families) of Limousin fetuses (combination 1, n = 3 heifers; combination 2, n = 2 heifers) or three half-sibling combinations (i.e, families) of Ayrshire fetuses (combination 3, n = 3 heifers; combination 4, n = 1 heifer; combination 5, n = 1 heifer). Hence,

TABLE 1. Least squares means of gestation length and calf birth weight and of milk yield and of fat content during the first 20 wk postpartum for Ayrshire dams bearing Ayrshire or Limousin fetuses.

	Breed of fetus			
	Ayrshire (n = 12)		Limousin (n = 11)	
	$\bar{X}$	SEM	$\bar{X}$	SEM
Gestation length,[1] d	280.2[a]	2.2	297.4[b]	2.5
Calf birth weight,[1] kg	35.4[a]	1.2	44.2[b]	1.4
Milk yield, kg/d	20.8[c]	.8[2]	18.1[d]	.8[2]
Milk fat, %	4.0	.1[2]	3.9	.1[2]

[a,b]Means with different superscripts differ ($P<.01$).

[c,d]Means with different superscripts differ ($P<.05$).

[1]Data from two Ayrshire dams that had stillborn calves at 255 and 263 d of gestation were excluded.

[2]SEM values are approximate, conservative, and similar for each group.

TABLE 2. Least squares ANOVA of milk production in Ayrshire heifers bearing Ayrshire or Limousin fetuses.

Source of variation	df	MS	Error term
Breed of fetus	1	335.5[a]	Heifer (breed)
Heifer (breed)	21	71.4[b]	Residual
Days	3	94.3[b]	Residual
Breed × day homogeneity of regression	3	1.4	Residual
Residual	187	2.7	

[a]$P<.05$.

[b]$P<.01$.

variation due to family of fetuses within breed was included in the mathematical model, and the experimental design was a split-split-plot. Repeated measurements over time were taken, and day (or week) was considered as a continuous independent variable (11). Each response was characterized by a time trend that was analyzed by polynomial regression. Tests of homogeneity of regression were used to detect differences in time trends for milk yield and endocrine responses between Ayrshire heifers carrying Limousin or Ayrshire fetuses. Data were analyzed relative to the day of parturition.

RESULTS

Physiological and Production Responses

Ayrshire dams bearing Limousin fetuses had longer ($P<.01$) gestation and heavier ($P<.01$) calves at birth than those bearing Ayrshire fetuses (Table 1). These differences in gestation length and calf birth weight remained significant ($P<.05$) even when data from two Ayrshire dams that had stillborn Limousin calves were included in the analysis.

Milk production of Ayrshire dams that had Ayrshire calves was 19.5 kg during wk 1 postpartum, peaked at 24.5 kg on wk 5, and decreased progressively to 19 kg by wk 20 (Figure 1). Lactation curve of Ayrshire dams that had Limousin calves was similar ($P>.1$) to that of the control group. However, daily milk production throughout the first 20 wk postpartum was approximately 2 to 3 kg lower ($P<.05$) in Ayrshire dams that had Limousin calves than in those that had Ayrshire calves (Figure 1; Tables 1 and 2). Fat content of milk did not differ ($P>.1$) between groups.

Endocrine Responses

Prepartum mean concentrations of progesterone and estrone did not differ ($P>.05$; Tables 3 and 4) between groups. However, breed of fetus carried during gestation influenced the profiles of prepartum plasma concentrations of progesterone and estrone in dams (Table 3; Figure 2). In Ayrshire dams carrying Ayrshire fetuses,

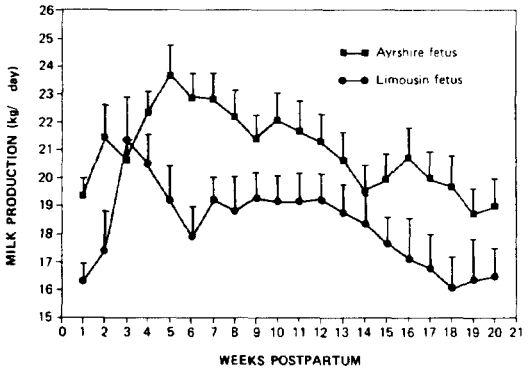

Figure 1. Least squares means of milk production during the first 20 wk postpartum in Ayrshire dams that had Limousin or Ayrshire calves.

TABLE 3. Least squares ANOVA of periparturient endocrine responses in Ayrshire heifers bearing Ayrshire or Limousin fetuses.

	Progesterone		Estrone		bPL[1]		PGFM[1]		
Source of variation	df	MS	df	MS	df	MS[2]	df	MS[2]	Error term
Breed of fetus	1	16.9	1	.25	1	2.3	1	20.7[a]	Family of fetuses
Family of fetuses (breed)	3	18.6	3	6.4	3	11.5[a]	3	1.5	Heifer (family, breed)
Heifer (family, breed)	5	20.5[b]	5	2.5[b]	5	1.6[b]	5	2.6	Residual
Days	3	17.9[b]	2	34.5[b]	4	7.6[b]	3	12.2[b]	Residual
Breed × days homogeneity of regression	3	4.0[a]	2	.8[b]	4	1.3[b]	3	3.7	Residual
Residual	154	1.3	165	.1	173	.2	164	1.5	

[a]$P<.05$.

[b]$P<.01$.

[1]bPL = Bovine placental lactogen; PGFM = 15-keto-13,14-dihydroprostaglandin $F_{2\alpha}$.

[2]MS × 10^5.

progesterone concentrations remained at approximately 5 ng/ml between d –21 and –6 and decreased thereafter. However, in Ayrshire dams carrying Limousin fetuses a progressive decrease ($P<.05$) in progesterone concentrations from 6 to 4 ng/ml occurred between d –21 and –10. Thereafter, progesterone concentrations, which were lower in dams carrying Limousin fetuses, decreased by d –2 as in the other group. A continuous increase ($P<.01$) was noted in plasma estrone concentrations during the last 3 wk prepartum. Between d –21 and –10, plasma estrone concentrations were higher ($P<.01$) in Ayrshire dams bearing Limousin fetuses than in those bearing Ayrshire fetuses. During the last 10 d prepartum, the increase in plasma estrone concentrations was similar in both groups.

TABLE 4. Least squares means of periparturient hormone concentrations (ng/ml) in Ayrshire dams bearing purebred Ayrshire or Limousin fetuses.

	Breed of fetus		
Hormone	Ayrshire	Limousin	SEM[1]
Progesterone	4.77	3.42	.44
Estrone	.98	1.20	.21
bPL[2]	.15	.25	.07
PGFM[3,a]	.41	.21	.05

[a]$P<.05$.

[1]SEM values are approximate, conservative, and similar for each group.

[2]bPL = Bovine placental lactogen.

[3]PGFM = 15-keto-13,14-dihydroprostaglandin $F_{2\alpha}$.

The peripartum plasma concentrations of bPL in the dams averaged .23 ng/ml on d –15, increased to peak values of .48 ng/ml on d –6, decreased progressively to .10 ng/ml on day of parturition, and were undetectable thereafter ($P<.01$; Table 3). The profiles of bPL concentrations differed ($P<.01$) between groups. Within each breed of fetus carried, however, families of fetuses accounted for a large portion of the variation (Table 3). Differences in bPL concentrations (Figure 3) were detected ($P<.05$) between Ayrshire dams bearing the two different full-sib combinations of Limousin fetuses (mean bPL, 84 vs. 492 pg/ml) but not among the three half-sib combinations represented in Ayrshire dams bearing Ayrshire fetuses (mean bPL, 154 vs. 168 vs. 119 pg/ml).

In both groups of Ayrshire dams, PGFM concentrations increased to nearly 1500 pg/ml on the day of parturition and then decreased progressively to basal value (50 to 70 pg/ml) by d 15 postpartum ($P<.01$; data not shown). Although profiles of PGFM concentrations were similar ($P>.1$) between groups, mean PGFM concentrations were consistently lower ($P<.05$) in heifers that carried Limousin calves than in those that carried Ayrshire calves (Table 4).

On a within-heifer basis, concentrations of bPL and progesterone were correlated positively ($r = .33$; $P<.01$) whereas those of estrone and progesterone were correlated negatively ($r = -.36$; $P<.01$). Among the 10 heifers, mean

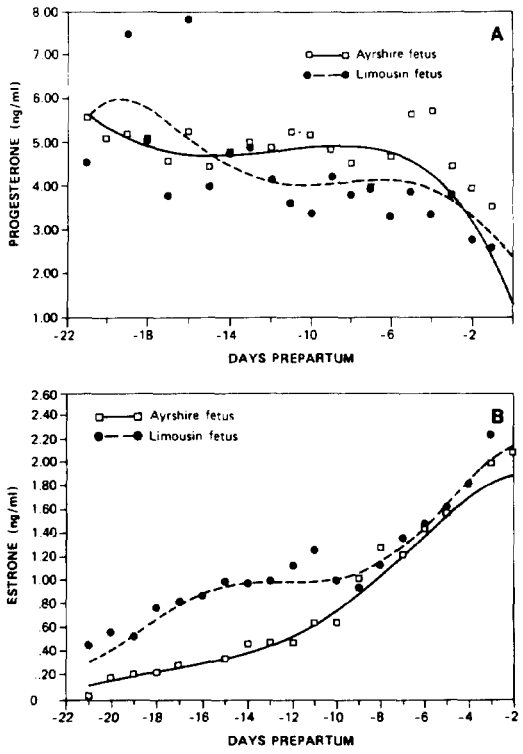

Figure 2. Least squares regressions and least squares means of prepartum (parturition, d 0) profiles of progesterone (panel A) and estrone (panel B) concentrations in Ayrshire dams carrying Limousin or Ayrshire fetuses.

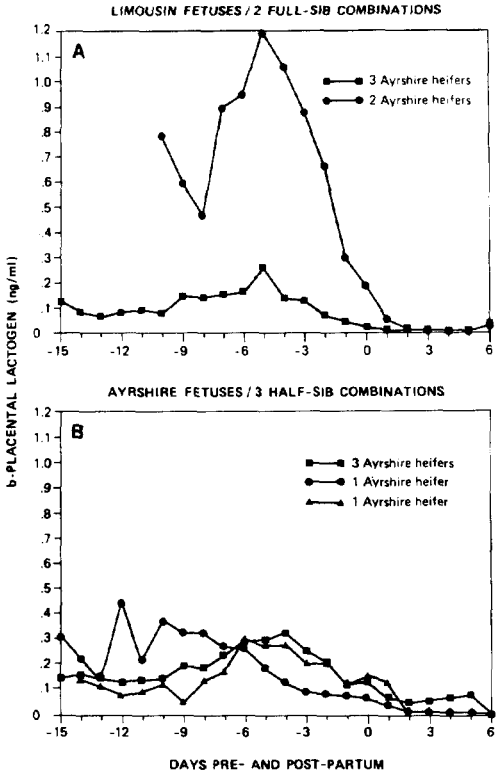

Figure 3. Peripartum profile of bovine placental lactogen in Ayrshire dams carrying different families of Limousin (full sibling, panel A) or Ayrshire (half-sibling, panel B) fetuses. Number of heifers carrying each family of fetus is indicated in legend.

bPL and estrone concentrations were correlated positively (r = .89; $P<.01$). The positive correlation between mean bPL (r = .51) or mean estrone (r = .51) concentrations and calf birth weight were not statistically significant ($P=.12$). Mean PGFM concentrations were correlated positively (r = .72; $P<.05$) with milk production.

DISCUSSION

Milk production, calving ease and days open (1, 14, 22, 23) as well as gestation length and calf birth weight (11) are affected by the genotype of the fetus. Through the use of embryo transfer, present results confirm earlier data indicating that gestation length and calf birth weight are affected especially when the breeds of the donor and that of the recipient are different (16, 17). Present data obtained from a limited number of animals under field conditions also provide evidence that the ensuing lactation of the dam may be altered by the breed of the fetus carried.

As observed by King et al. (16, 17), the longer gestation in Ayrshire dams carrying Limousin fetuses supports the theory that the fetus is largely responsible for initiating parturition (21) and that fetal genotype is the principal regulator of the duration of pregnancy (18). At variance with King et al. (17), gestation length of Limousin calves carried by Ayrshire heifers appeared to be longer than that of nonembryo transfer Limousin calves (gestation length = 287.3 ± 5.7 d; 20). This suggests that maturation of the hypophyseal-adrenal axis of Limousin fetuses may be slower when gestation occurs in Ayrshire recipients or that the responsiveness of Ayrshire recipients to endocrine signals originating from Limousin fetuses

is decreased. Since birth weight of Limousin calves in the present study was comparable to that of nonembryo transfer Limousin calves (20), the maternal environment provided by Ayrshire heifers probably limited the growth of Limousin fetuses to some extent. Anthony et al. (2) reported that limitation in the maternal environment restricts growth of high birth weight-sired male calves.

The marked increase in plasma estrone concentrations in concert with decreasing progesterone concentrations during the last weeks of pregnancy was in agreement with earlier reports (9, 11). Differences in prepartum profiles of estrone and progesterone concentrations are directly attributable to the breed of service sire (11). Likewise, in the present experiment, breed of fetus carried by Ayrshire dams accounted for a significant portion of the variation in peripheral estrone and progesterone concentrations. Chorionic gonadotropin-like proteins with luteotrophic activities are present in extracts of bovine cotyledons (4), and Kitts et al. (18) provided evidence that fetal production of steroids (androgen and estrogen) is governed largely by the fetal genotype in sheep. Differential production of chorionic gonadotropin-like proteins and of estrogens by cotyledons (15) of Limousin and Ayrshire fetuses during the prepartum period may contribute to some of the difference observed in peripheral concentrations of progesterone and estrone in Ayrshire dams of the two groups.

The nearly 13% lower milk production of Ayrshire heifers that had Limousin calves, compared with those that had Ayrshire calves, is consistent with the hypothesis that the conceptus (or the sire of fetus) may affect subsequent lactational performances of the dam (1, 14, 22, 23, 25). Supporting that hypothesis, Guilbault et al. (11) reported that breed of service sire influences hormone concentrations of both maternal (progesterone, PGFM) and conceptus (estrogen) origin. Differences in prepartum steroid concentrations in the present experiment may be related to observed differences in subsequent milk production. The association of a decreasing progesterone coincident with rising estrogen concentrations appears to be a trigger mechanism for lactogenesis (8). Relative to parturition, Ayrshire heifers carrying Limousin fetuses had a more rapid decrease in progesterone concentrations and an earlier rise in estrone concentrations than those carrying Ayrshire fetuses. This suggests that the process of lactogenesis may have been initiated earlier in Ayrshire heifers carrying Limousin fetuses. Because gestation was longer and milking was delayed in this group, the mammary gland could not be as functional during the ensuing lactation. This is supported by visual observation that prepartum distention of the mammary gland was appreciably less in Ayrshire dams carrying Limousin fetuses than in those carrying Ayrshire fetuses. Furthermore, this is consistent with the observation that initiation of parturition with dexamethasone and prostaglandin $F_{2\alpha}$ at 288 d of gestation in Ayrshire dams carrying Limousin fetuses (n = 8) completely eliminated the detrimental effect of a longer gestation and resulted in normal lactational performances (Guilbault and Roy, unpublished observations). Conversely, the negative effect on milk production of the large birth weight of Limousin calves and of a higher incidence of dystocia in Ayrshire recipients cannot be ruled out. Thatcher et al. (25) reported a positive curvilinear relationship between calf birth weight and milk production in Holstein and Jersey cows.

To the best of the authors' knowledge, this is the first report of bPL concentrations in maternal circulation from repeated measurements taken on the same animals. In agreement with Beckers et al. (3), but at variance with Byatt et al. (6), a time trend in bPL concentrations was found that increased during the last weeks of pregnancy. In agreement with previous observations on placental lactogen in sheep (7), maternal bPL concentrations started to decline 5 to 6 d prior to parturition and were undetectable thereafter. Immunohistochemical techniques show that bPL is produced in the fetal part of the placentome by the binucleate cells of the trophectoderm (27). The prepartal decline of bPL initiated 5 to 6 d prior to parturition probably reflects a progressive loss of function in the binucleate cells near term.

As for estrogens (11), two lines of evidence suggest that bPL also may reflect the inherent variability of the embryo (or the service sire) to affect the maternal unit. Families of fetuses accounted for a significant portion of the variation in bPL concentrations and the two full-sib families of Limousin fetuses had distinct prepartum profiles of bPL concentrations. Also,

bPL and estrone concentrations were closely and positively correlated. Collectively, these results suggest that the fetal genotype regulated the production of placental lactogen.

The biological activities of bPL in vitro are essentially equivalent to that of bovine prolactin and are even higher than that of bST (3). Development of the mammary gland, which is closely associated with development of the fetus, is initiated during the second trimester of gestation (25), and measurable amounts of bPL are detected in maternal circulation as early as 110 d of gestation (3, 6). Sampling of animals during the last 2 wk of pregnancy may have precluded our ability to detect any relationship between bPL concentrations and milk production in the present experiment. Genotypic differences affecting birth weight are manifested before 200 d of gestation (2). Also, bPL may be only one of the component of a complex array of hormones that are implicated in mammogenesis and lactogenesis (8), and no direct relationship can be established.

The significance of the positive relationship between PGFM concentrations and milk production is still unclear. Nevertheless, in agreement with an earlier report (12), present results show that the genotype of the conceptus has a carry-over effect on postpartum PGFM concentrations of the dam and that elevated concentrations of PGFM are not necessarily due to a high calf birth weight (19).

In summary, present results with a limited number of animals provide evidence that the breed of fetus carried during gestation may influence subsequent lactational performances of Ayrshire females and that this is associated with alterations of peripartum hormonal profiles. Potential effects of the fetus should be considered in the embryo transfer business especially when donor breed and recipient breed are different.

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