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Role of the Central Nervous System in the Regulation of Pregnancy, Parturition and Lactation in Beef Heifers

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Abstract
Progesterone secretion is crucial for maintaining pregnancy to parturition in mammalian species, and in cattle the corpus luteum is the primary source of this hormone. This study determined the roles of prolactin (PRL), growth hormone (GH) and luteinizing hormone (LH) in the luteotropic process in beef heifers hypophyseal stalk-transected (HST, n = 7) or sham operated on (SOC, n = 9) during midgestation. The main finding was that endogenous PRL and GH maintained progesterone secretion in HST heifers similar to that in SOC throughout pregnancy. Serum PRL averaged 37 vs 187 and GH 2 vs 4 ng/ml in HST compared with SOC, whereas LH abruptly decreased to undetectable levels after HST compared with modest 0.4 ng/ml in SOC heifers. The second finding was that parturition and lactation occurred in HST heifers with calf delivery induced to occur at the same time as SOC. Milk production in HST animals was severely limited, and postpartum estrus obliterated compared with SOC. The suckling stimulus sustained milk ejection in HST heifers in spite of diminished PRL and GH secretion. The results suggest that PRL, GH and possibly placental lactogen are luteotropic during pregnancy in cattle.

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Lloyd L. Anderson, distinguished professor of animal science

Summary
Progesterone secretion is crucial for maintaining pregnancy to parturition in mammalian species, and in cattle the corpus luteum is the primary source of this hormone. This study determined the roles of prolactin (PRL), growth hormone (GH) and luteinizing hormone (LH) in the luteotrophic process in beef heifers hypophyseal stalk-transected (HST, n = 7) or sham operated on (SOC, n = 9) during midgestation. The main finding was that endogenous PRL and GH maintained progesterone secretion in HST heifers similar to that in SOC throughout pregnancy. Serum PRL averaged 37 vs 187 and GH 2 vs 4 ng/ml in HST compared with SOC, whereas LH abruptly decreased to undetectable levels after HST compared with a modest 0A4 ng/ml in SOC heifers. The second finding was that parturition and lactation occurred in HST heifers with calf delivery induced to occur at the same time as SOC. Milk production in HST animals was severely limited, and postpartum estrus obliterated compared with SOC. The suckling stimulus sustained milk ejection in HST heifers in spite of diminished PRL and GH secretion. The results suggest that PRL, GH and possibly placental lactogen are luteotropic during pregnancy in cattle.

Introduction
Progesterone secretion is crucial for maintaining pregnancy to parturition in mammalian species. Ovarian production of progesterone is required for at least 200 days of the approximate 280-day gestation in cattle; ovariectomy at 48-117 days causes abortion within 96 hours whereas ovarian removal at 139-268 days results in fewer delivered living calves and 100% retained fetal membranes. Calving difficulties, including uterine inertia and partial cervical dilation are common. The corpus luteum in the ovary is the major source of progesterone during pregnancy in cattle.

Prolactin (PRL) and luteinizing hormone (LH) play pivotal roles in the luteotropic process, and progesterone produced by the corpus luteum might function as a universal luteotropic hormone by controlling its own production through an autocrine mechanism. A luteal microsomal 32-kilodalton phosphoprotein, a PRL receptor associated protein (PRAP), is expressed in the corpus luteum of the rat, mouse, hamster, cow, pig, and human. Coexpression of PRL-receptor long (PRL-RL) and short (PRL-RS) forms is elevated during pregnancy with large luteal cells expressing the bulk of PRL-R.

R. Bovine tissues contain two transcripts for the PRL-R, a short form that includes an additional 39 bases at a position identical to the deviation from the long form found in rodents and sheep.

In cattle, our evidence indicates that the corpus luteum develops and secretes progesterone after HST early (day 2) in the estrous cycle. Progesterone peaks at day 12 and decreases to a low level by day 20, but these HST beef heifers remain anovulatory thereafter. Progesterone secretion continues beyond 48 days in HST-hysterectomized heifers.

This study focuses on the role of PRL, GH and luteinizing hormone (LH) in corpus luteum function during pregnancy in HST beef heifers.

Materials and Methods

Animals and surgery
Crossbred (Hereford × Aberdeen Angus) heifers 15-30 months old and weighing 240-410 kg were bred by artificial insemination. The day of breeding was designated day 0. The heifers were hypophyseal stalk-transected (HST, n = 7) during midgestation by a supraorbital approach that we described previously. Briefly, anesthesia was induced by intravenously-injected thiopental sodium (11 mg/kg body wt) for intubation with an inflatable endotracheal catheter. The heifers were maintained on a closed-circuit system of halothane (2-4%) and oxygen (800-1800 ml/min) and suspended in ventral recumbency by canvas belts. An animal head restrainer, attached to the front of a cattle squeeze chute, permitted the head to be raised, lowered, tilted and turned to the desired position for neurosurgical intervention. Cortisone acetate (100 mg) was intramuscularly-injected before surgery was begun, and 20% mannitol was intravenously-infused for 20 minutes immediately preceding the opening of the dura mater and the lifting of the left cerebral hemisphere to expose the hypophyseal stalk. Surgical intervention required 5-6 hours. After the hypophyseal stalk was severed by dissection with spherical-tipped platinum probes, a nylon disc (9A5 mm diameter and 0A45 mm thickness) was inserted between the severed ends of the tubular stalk to prevent vascular regeneration. Sham operation control (SOC, n = 9) included all surgical procedures except transection of the stalk. After recovery, all heifers were maintained under pasture conditions.

Anterior vena cava blood was withdrawn every fourth day beginning on day 100 of pregnancy and continuing through day 330 from breeding. Blood was cooled on ice, allowed to clot at 15EC, and then centrifuged at 5E for 20 min at 1500 x g. Serum was stored frozen (-20EC) for hormone assays.
Hormone radioimmunoassay (RIA)

Progesterone RIA was identical to that we described previously with the exception of the extraction procedures. Serum aliquots (200 µl) of each unknown, in duplicate, were added to two tubes without tracer and one tube containing dried tracer (5000 cpm; [1, 2, 6, 7-N\(^3\)H]-progesterone; 97A0 Ci/mmol) to determine extraction efficiency. Two milliliters of benzene-hexane (1:2) were added to all tubes. Each tube was shaken vigorously for 30 sec, and then was placed on dry ice to freeze the aqueous phase. The organic phase of the extracts containing \(^3\)H-progesterone was decanted into scintillation vials whereas the extracts from the remaining two aliquots of each unknown were decanted into assay tubes and dried for subsequent RIA. Preliminary experiments revealed little variance in procedural losses (94A6 \(\pm\) 0A9% extraction efficiency). Assay sensitivity was 50 pg/tube. Inter-assay and intra-assay coefficients of variation were 11A7% (n = 28) and 8A5% (n = 6), respectively.

The estradiol-17ß (E\(_1\)-17ß) and estrone (E\(_2\)) RIA was a modification of our procedure to allow a more sensitive determination of estradiol in ovine and bovine serum. Three thousand dpm [2, 4, 6, 7-\(^3\)H]-estradiol-17ß (114 Ci/mmol) was added to 2 ml serum to facilitate the determination of procedural losses. The samples were extracted twice with 3 volumes of double-distilled benzene, and the final benzene extract washed twice with 0A1 vol deionized water. Following each extraction, an aqueous-organic solvent phase separation was achieved by centrifugation at 500 x g for 10 min and the organic solvent removed by aspiration. Assay sensitivity was about 2 pg. Intraassay coefficients of variation for E\(_1\) and 17ßE\(_2\) were 3A0 and 2A9%, respectively. Inter-assay coefficients of variation for E\(_1\) and 17ßE\(_2\) were 7A1 and 9A5%, respectively.

LH was measured in 100- to 300-µl aliquots of serum, in duplicate, by using highly purified bovine LH (bLH) for labeling with \(^125\)I (IMS 30) and for standards (36 pg to 20 ng). Assay sensitivity was 0A2 ng/ml. Intra- and inter-assay coefficients of variation were 8A2 and 11A2%, respectively.

PRL was measured in 20- to 100-µl aliquots of serum, in duplicate, by using highly purified ovine PRL (oPRL) for labeling with \(^125\)I and purified bovine PRL (bPRL) for standards (40 pg to 20 ng). Assay sensitivity was 0A28 ng/ml. Intra- and inter-assay coefficients of variation were 4A9 and 9A4%, respectively.

GH was measured in 100 µl aliquots of serum in duplicate using highly purified bGH (USDA-bGH-1-1, 3A2 IU/mg) for labeling with \(^125\)I by the chloramine T method, highly purified bGH for standards (0A125-2 ng), and incubation at 4EC for 72 h by procedures similar to those we described previously. Assay sensitivity was 0A125 ng/tube. Intra- and inter-assay coefficients of variation were 3A5% and 11A2%, respectively.

Parturition

HST and SOC heifers were closely monitored near the time of expected parturition (day 280 in this herd). With onset of labor, manual assistance was given when required. In animals showing no signs of spontaneous delivery, parturition was induced by intramuscular injection of dexamethasone and subsequent oxytocin treatment to ensure safe delivery of a calf, or by cesarean section.

Lactation and milk composition

Calves were allowed to suckle their dams throughout 30 weeks. Milk production by HST and SOC heifers was determined at weekly intervals. Calves were separated from their dams for a 24-h period, and the cow was milked twice (0800 and 1600 h) during that period. Aliquots of milk (n = 116) from these animals were analyzed for fat, protein, lactose, and total solids by absorption of infrared light, and the constituents expressed as percentage composition of whole milk.

Histology

Postmortem examination of each animal confirmed the completeness of stalk transection. The nylon disc was in the proper location and had prevented vascular regeneration of the stalk in each heifer. Pituitary glands from HST and SOC heifers were cut at 6 µm and stained with performic acid-Alcian blue-periodic acid-Schiff-orange G, whereas other sections were stained with hematoxylin and eosin.

Statistical analysis

Experimental units in this study were the individual heifers, each assigned to treatments at random. Least-squares analyses were based on a weighted average of sample variance for experimental and control groups. Hormone data were analyzed by a split-plot analysis using a one-way analysis of variance, and Student's t tests for continuous variables were used for comparisons between groups. Data are presented as geometric mean \(\pm\) S.E.M., and statistical significance was concluded when \(P < 0A05\).

Results

Pregnancy and parturition after HST

Six of 7 HST heifers delivered living calves (Table 1). There was no evidence of onset of labor in 4 HST heifers, and parturition was induced in these animals by intramuscular injection of dexamethasone, followed approximately 30 h later with an intravenous injection of oxytocin (Tables 1 and 2). Delivery required no assistance in 8 of 9 control animals, but cesarean section was necessary in one SOC heifer.

Lactation and postpartum estrus after HST

Lactation was maintained in both HST and SOC (Table 1) animals.
None of the HST heifers exhibited a postpartum estrus during periods exceeding 300 days (Table 2). SOC heifers returned to estrus within 2 months after parturition.

**Calf performance and milk production**

Birth weight of calves delivered from HST heifers was similar (P > 0.05) to that produced by SOC (Tables 1 and 2). By 100 days after birth, body weight and growth rate of calves from HST heifers was less (P < 0.001; P < 0.025, respectively) than in calves from SOC. Limited neonatal growth of calves born to HST heifers resulted primarily from decreased milk production by the dams. Milk production in the first week postpartum was less (P < 0.001) in HST than in SOC females in the first week postpartum (Fig. 1); paired comparisons indicated reduced (P < 0.001) milk secretion in HST compared with SOC throughout the 30 wk lactation. The results indicate that E2 and 17βE2 and prolactin secretion in cattle is tonically inhibited by the hypothalamus and remains seasonally regulated. A similar transient increase in PRL secretion occurs soon after hypophyseal stalk separation in ewes during the anestrous and the breeding season. HST beef calves had consistently lower serum PRL (5 ng/ml) compared with SOC (40 ng/ml), but both groups remained acutely sensitive to seasonal changes throughout the year with peak hormone concentration in summer and reaching a nadir in winter. In this study, serum PRL was sevenfold greater (37 ng/ml) in HST heifer calves during pregnancy compared with prepubertal HST heifer calves, whereas LH decreased abruptly after HST to undetectable levels after HST and remained consistently lower than SOC throughout the remainder of gestation. Likewise, GH concentration remained lower (P < 0.05) in HST than SOC during early lactation.

**Discussion**

The main finding in this study was that progesterone secretion in HST beef heifers was maintained at a similar level to that seen in SOC throughout pregnancy. Although PRL secretion in cattle is tonically inhibited by the hypothalamus and remains significantly greater the first 14 days after HST than that in SOC, circulating PRL concentration gradually decreases lower but remains seasonally regulated. A similar transient increase in PRL secretion occurs soon after hypophyseal stalk separation in ewes during the anestrous and the breeding season. HST beef calves had consistently lower serum PRL (5 ng/ml) compared with SOC (40 ng/ml), but both groups remained acutely sensitive to seasonal changes throughout the year with peak hormone concentration in summer and reaching a nadir in winter. In this study, serum PRL was sevenfold greater (37 ng/ml) in HST heifer calves during pregnancy compared with prepubertal HST heifer calves, whereas LH decreased abruptly to undetectable levels after HST at midgestation.

Dopamine may be involved in tonic regulation of PRL secretion in rats, pigs, sheep, cattle, and monkeys based on elevated circulating PRL concentration after HST and acute stimulatory effects of haloperidol and α-methyl-p-tyrosine on PRL secretion. The maintenance of progesterone secretion by aging corpora lutea with daily PRL treatment in hysterectomized-hypophysectomized animals provides further evidence for PRL’s luteotropic action. Bovine PL (bPL), a glycosylated hormone produced by trophoblast binucleate cells only during pregnancy, and bovine GH from the anterior pituitary are members of the same gene family.
family and have structural and functional similarities. Ovine PL and bovine PL can act through PRL-R and elicit PRL-like effects in ovine and bovine mammary gland and rat Nb2 lymphoma cells. Bovine PL may act through this putative unique receptor, through the PRL-R and(or) through a heterodimer of the PRL-R and GH-R.

Bovine PRL receptors (bPRL-R) in the bovine corpus luteum, mammary gland and liver have been measured. There also is evidence for bovine GH receptor (bGH-R) and bPRL-R transcripts in bovine extraembryonic membranes and in the glandular uterine endometrium, but much lower levels of both receptor mRNAs are found in the caruncles. Bovine corpus luteum and endometrium have a unique mRNA that hybridizes with a cDNA for bGH-R. The giant cells of the bovine corpus luteum have been shown to be rich in GH-R message and to stain positively by immunohistochemistry for the presence of cell surface GH-R. Thus, the biological activity of these related hormones not only depends on receptor distribution and affinity of hormone for the receptor, but also on transmission of signal in response to binding.

The second finding in this study was that pregnancy continued, and parturition and lactation occurred in beef heifers HST at mid-gestation (138-201 days), with calf delivery occurring at the same time as SOC (286 days). Although HST heifers maintained pregnancy, hormonally induced parturition (dexamethasone and oxytocin) was required in most animals; milk production was severely limited during the 30 weeks of lactation, and postpartum estrus was obliterated compared with SOC. Studies in dairy cows have demonstrated that bPL treatment increases milk production, suggesting that bPL may have GH-like galactopoietic actions. Long-term effects of bGH treatment in lactating cows suggest that bGH acts primarily by changing tissue responsiveness to homeostatic signals so that a greater proportion of nutrients is partitioned for increased milk yield. Although circulating concentrations of estrogen, progesterone, bGH, bPRL and possibly bPL were adequate to stimulate mammmogenesis during the later half of pregnancy in HST heifers in the present study, the markedly reduced milk production during lactation suggests that decreased circulating concentrations of PRL and GH were the primary limiting factors compared with SOC heifers.

HST heifers remained anovulatory by blocking GnRH secretion to pituitary gonadotropes, whereas postpartum estrus and ovulatory cycles resumed within 2 months in SOC animals. Although ovarian follicles abruptly regressed in HST heifers, the corpus luteum was maintained similarly to that seen in SOC throughout pregnancy. Postpartum, corpus luteum regression was abrupt and ovarian follicular growth arrested for at least 300 days in HST compared with SOC heifers.

**Implications**

The results from this study show that endogenous PRL, GH and possibly bPL secretion maintained corpus luteum function and progesterone secretion in beef heifers HST at midgestation; LH decreased to undetectable levels. Furthermore, the HST heifers delivered live calves and sustained a modest lactation during 30 weeks of suckling by the calves. The decreased milk production in HST cows corresponded with significantly decreased serum concentrations of PRL and GH and presumably decreased cortisol release around parturition and lactation compared with that in SOC heifers. HST blocked GnRH-induced gonadotropin secretion with the cows remaining anovulatory for more than 300 days whereas estrous cycles had resumed in SOC animals by 2 months postpartum.

**Reference**

Table 1. Pregnancy, parturition, lactation, and calf development in HST and SOC beef heifers.

<table>
<thead>
<tr>
<th>Heifer no.</th>
<th>Day of surgery</th>
<th>Duration of pregnancy (days)</th>
<th>Type of delivery</th>
<th>Lactation during 30 weeks</th>
<th>Calf</th>
<th>Body weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sex</td>
<td>Birth</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100 days of age</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Gain</td>
<td>(kg/day)</td>
</tr>
</tbody>
</table>

HST
40  201  289  induced\(^H\)  +  &  34A02  82A29  0A48
70  200  280  unassisted  +  &  24A95  66A53  0A42
74  161  293  induced\(^H\)  +  %  41A75  117A29  0A76
71  161  284  induced\(^H\)  +  %  34A02  97A19  0A63
33  149  283  unassisted  +  %  34A02  97A19  0A63
73  143  287  induced\(^H\)  +  %  31A75  75A05  0A43

SOC
44  205  284  unassisted  +  &  36A29  143A10  1A07
47  201  286  unassisted  +  &  36A29  131A65  0A95
38  200  285  unassisted  +  %  34A02  145A26  1A11
36  162  287  unassisted  +  %  29A48  93A09  0A64
148  160  286  unassisted  +  &  41A73  152A57  1A11
75  159  295  cesarean  %  42A63  84A77  0A42
44A  145  288  unassisted  +  &  38A55  108A54  0A70
149  141  281  unassisted  +  &  35A38  113A71  0A78
45  140  283  unassisted  +  &  29A48  115A79  0A86

\(^*\) Progesterone concentration in peripheral blood serum from 35 bleedings at 4-day intervals averaged 0.9 \(\pm\) 0.10 ng/ml \((\mp\text{ S.E.M.) from day 100 to day 236; pregnancy failed.})

\(^H\) Dexamethasone intramuscularly followed by oxytocin intravenously at time of delivery.

\(^\prime\) Calf died within 5 minutes after delivery.
<table>
<thead>
<tr>
<th></th>
<th>No. of heifers</th>
<th>Calf</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pregnancy duration (days)</td>
<td>Experiencing</td>
</tr>
<tr>
<td>HST 286 + 1A9</td>
<td>286 + 1A9</td>
<td>4 of 6</td>
</tr>
<tr>
<td>SOC 286 + 1A3</td>
<td>286 + 1A3</td>
<td>1&lt;sup&gt;H&lt;/sup&gt; of 9</td>
</tr>
</tbody>
</table>

<sup>1</sup> Pregnancy failed after surgery in one heifer.

<sup>H</sup> Cesarean.

<sup>a</sup> P < 0A025.

<sup>b</sup> P < 0A001.
Table 3. Serum LH concentration before surgery, and after SOC and HST at midgestation, parturition and early lactation in beef heifers. Values are means ∀ S.E.M.

<table>
<thead>
<tr>
<th>Reproductive State</th>
<th>Day</th>
<th>LH (ng/ml)</th>
<th>SOC (n = 6)</th>
<th>HST (n = 6)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Presurgery (n = 12)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pregnancy</td>
<td>-40</td>
<td>0A27 ∀ 0A01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-32</td>
<td>0A28 ∀ 0A01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-24</td>
<td>0A32 ∀ 0A04</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>-16</td>
<td>0A29 ∀ 0A01</td>
<td></td>
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<td></td>
<td>-8</td>
<td>0A33 ∀ 0A06</td>
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<td>0</td>
<td>0A63 ∀ 0A32</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>0A37 ∀ 0A01</td>
<td>ND&lt;sup&gt;a&lt;/sup&gt;</td>
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</tr>
<tr>
<td></td>
<td>16</td>
<td>0A31 ∀ 0A02</td>
<td>ND</td>
<td></td>
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<tr>
<td></td>
<td>24</td>
<td>0A28 ∀ 0A01</td>
<td>ND</td>
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<td></td>
<td>32</td>
<td>0A44 ∀ 0A14</td>
<td>ND</td>
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</tr>
<tr>
<td></td>
<td>40</td>
<td>0A31 ∀ 0A03</td>
<td>ND</td>
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<td>48</td>
<td>0A37 ∀ 0A01</td>
<td>ND</td>
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<td></td>
<td>56</td>
<td>0A36 ∀ 0A06</td>
<td>ND</td>
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<tr>
<td></td>
<td>64</td>
<td>0A29 ∀ 0A01</td>
<td>ND</td>
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<tr>
<td></td>
<td>72</td>
<td>0A30 ∀ 0A01</td>
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<td></td>
<td>80</td>
<td>0A29 ∀ 0A01</td>
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<tr>
<td></td>
<td>88</td>
<td>0A31 ∀ 0A04</td>
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<tr>
<td></td>
<td>96</td>
<td>0A29 ∀ 0A01</td>
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<td></td>
<td>104</td>
<td>0A28 ∀ 0A01</td>
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<td></td>
<td>112</td>
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<td>Lactation</td>
<td>128</td>
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<td></td>
<td>136</td>
<td>0A39 ∀ 0A09</td>
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<tr>
<td></td>
<td>144</td>
<td>1A48 ∀ 0A60</td>
<td>ND</td>
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</table>

<sup>a</sup>Not detectable (<0A2 ng/ml).
Figure 1. Milk production in HST (>) and SOC (M) beef heifers. Calves suckled their dams throughout this 30-week period. Dams were isolated from their calves once each week for 24 hours and were milked twice (0800 and 1600 h) during that period. The number of heifers is indicated in parentheses. Values are means ± S.E.M.

Figure 2. Concentration of progesterone (a), estrone (b), estradiol-17β (c), and prolactin (d) in peripheral serum at 4-day intervals in HST (>) and SOC (M) beef heifers during pregnancy, parturition, and lactation (day 0 = estrus). Three SOC heifers died within 3 days after surgery; postmortem examination revealed bleeding from the severed internal carotid in one animal and accumulation of blood in the cranial sinus from vasculature of the dura mater and calvarium in two heifers. The number of heifers is indicated in parentheses. Values are means ± S.E.M.