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Distribution and Repeatability of Anterior Pituitary Responses to GnRH and Relationship of Response Classification to the Postpartum Anovulatory Interval of Beef Cows^{1,2}

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ABSTRACT: Our objectives were to investigate the phenotypic variation in anterior pituitary responsiveness to GnRH (100 μ g, i.v.) of beef cows between d 5 and 8 postpartum, estimate repeatability, and determine the relationship between response classification and duration of the postpartum anovulatory interval (PPI). Brahman \times Hereford (F₁) cows (n = 137) and primiparous heifers (n = 58) were evaluated. Response classifications (Class) included peak LH (Low, Intermediate, or High; Class I) and time to peak LH (Early, 10 to 30 min or Late, 60 to 120 min; Class II). The independent effects of Class I and II on PPI were determined in 145 of 195 cows through twice-weekly serum samples analyzed for progesterone. For Class I, pituitary responses to GnRH approximated a normal distribution and, by definition, differed ($P < .001$) in magnitudes of peak LH and area under the curve (AUC). For Class II, 111 and 84 cows exhibited early and late peaks,

respectively; mean AUC was greater ($P < .05$) in cows exhibiting late compared with early peaks. Pretreatment LH ($P < .01$) and estradiol-17 β ($P < .004$) influenced responses in one or both response classes. Pluriparous cows had shorter ($P < .035$) PPI than primiparous cows. Class I did not influence the duration of the PPI; however, in Class II, cows with late peaks exhibited an average PPI that was 8 d shorter ($P < .025$) than in those with an early peak. To estimate repeatability of pituitary responses, 18 classified cows were subsequently rechallenge with GnRH at d 170 of gestation and at the next postpartum period. Although means for each of these challenges differed ($P < .05$) throughout in both Classes I and II, the small sample size used to make the estimate failed to yield significant ($P > .10$) interclass correlations. Nevertheless, overall results provide evidence that variability in individual pituitary responses to GnRH could be targeted as a selection marker to improve reproduction.

Key Words: Anterior Pituitary, GnRH, LH, Beef Cattle

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Introduction

Synthesis and secretion of LH are controlled by GnRH through receptor-mediated phenomena at the level of the gonadotrophs (Fink, 1988). External and internal factors, including steroid hormones, photoperiod, suckling, and energy balance, modulate this relationship. Because the magnitude of gonadotropin secre-

tion is central to the control of ovarian processes, identifying individuals with an inherently greater capacity to secrete gonadotropins under defined conditions could be a valuable selection tool for improving reproductive efficiency.

Under standardized physiological conditions, the between-animal variation in adenohipophyseal responsiveness to pharmacological doses of GnRH, which cause mobilization and secretion of all releasable pools of LH, exceeds the within-animal variation (Webb et al., 1977; Williams et al., 1982; Williams and Stanko, 1996). The intrinsic responsiveness to exogenous GnRH of male lambs from a genetically heterogeneous population was characterized, and this trait was then selected for over several generations. Both male and female offspring from these selected lines continued to exhibit the expected high or low responses to GnRH, with corresponding changes in endogenous gonadotropin secre-

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tion (Haley et al., 1989; Evans et al., 1991, 1994, 1995). Prolificacy of high-line ewe lambs was improved during the first two breeding seasons compared to that of low-line ewes (McNeilly et al., 1993).

The hypothesis for the study reported here was that phenotypic variation in anterior pituitary responsiveness to GnRH in cattle can serve as a physiological marker for reproductive efficiency. Our objectives were to identify subpopulations of beef cows that differ markedly in their responsiveness to GnRH based on two independently selected criteria, make preliminary estimates of repeatability, and determine their relationship to a single measure of efficiency, duration of the postpartum anovulatory interval (PPI).

Materials and Methods

Animal Model

The population of beef cows used in the current study was examined for anterior pituitary responsiveness to GnRH between d 5 to 8 postpartum to standardize physiological conditions and to attempt to maximize the sensitivity of the experimental model. This paradigm was chosen because of characteristic features associated with anterior pituitary gonadotrophs at or immediately following gestation (Nett, 1987) and the low probability (< 5%) of the presence of an estrogen-active, large follicle capable of ovulating after GnRH treatment (Ryan et al., 1994). At this time, previous exposure to high concentrations of gestational estradiol has severely diminished or depleted gonadotrophs of the alpha and beta subunits of LH (Nett, 1987). Parturition is followed by a variable rate of repletion of LH stores during the first 15 to 30 d postpartum (Kesler et al., 1977; Williams et al., 1982; Moss et al., 1985). Therefore, between d 5 to 8 postpartum, cows are in a repletion mode, and maximal releasable pools of LH are not expected for several more weeks in the population as a whole. The expected average peak response to a pharmacological challenge of GnRH would be between 4 and 8 ng/mL at this time (Williams et al., 1982). However, a few cows exhibit peaks of 20 to 25 ng/mL, and others exhibit either no response or one only slightly above baseline (Williams et al., 1982; Williams and Stanko, 1996). Therefore, we hypothesized that individual cow variability associated with gestational depletion of LH, or, conversely, variability in postpartum repletion rate, could serve as an exquisite model for estimating the "physiological fitness," and by indirect inference, genotypic fitness to secrete gonadotropin.

Classification Systems

For Class I, peak serum concentrations of LH after GnRH treatment for each animal were categorized as phenotypically High, Intermediate, or Low according to their relative difference from the mean of the population sample. A high response was represented by serum

LH concentrations > 1 SD above the mean, an intermediate response was within 1 SD, and low represented > 1 SD below the mean. This approach differs from that employed in sheep studies (Haley et al., 1989) in which male lambs exhibiting high (above the geometric mean response) or low (below the geometric mean response) responses were selected over several generations, bred to unselected ewes, and reproductive performance of female offspring from these lines were compared.

After initial analyses of LH responses, a second, independent classification system (Class II) was employed in addition to Class I. The system segregated cows on the basis of the time to peak LH concentration after GnRH treatment. This analysis was undertaken because of our observation that cows formed two natural response populations, those in which peak concentrations of LH occurred at 10 to 30 min (Early) and those that peaked at 60 to 120 min (Late).

Animals

Brahman × Hereford pluriparous cows (n = 137) and primiparous heifers (n = 58) were used. They were maintained on Coastal bermudagrass and kleingrass pasture and supplemented with cottonseed meal as needed to meet NRC (1984) requirements for lactating beef cows to maintain a body condition score between 5 and 6 on a scale of 1 to 9 (1 = emaciated and 9 = obese; Herd and Sprott, 1986). The study was carried out in three separate trials conducted during spring 1996 (n = 58), fall 1996 (n = 60), and spring 1997 (n = 77).

Experimental Procedures

All cows and heifers were treated with a single pharmacological dose of GnRH (100 µg, i.v.) on d 5, 6, 7, or 8 postpartum. Blood samples were collected by jugular or coccygeal venipuncture prior to the injection (time 0) and at 10, 30, 60, 120, and 240 min thereafter for determination of serum concentrations of LH. Progesterone and estradiol-17β were also measured in preinjection samples. Animals were weighed and assigned a body condition score at the time of injection and every 28 d throughout the trials.

Only 145 of the 195 cows were available to determine PPI. Twice-weekly blood samples were obtained during wk 1 to 14 postpartum or until two consecutive samples had serum concentrations of progesterone ≥ 1 ng/mL. Cows that had not ovulated by the end of the 14-wk period were assigned a PPI of 100 d (n = 4) and were included in the analyses.

Peak LH responses from 18 pluriparous cows from the first trial (spring 1996) were used to make preliminary estimates of repeatability of the characteristic using interclass correlation (r) as described by Bourdon (1997). Eighteen cows that had been classified previously as High (n = 9) or Low (n = 9) were treated with GnRH (100 µg, i.v.) on two additional occasions: 1) 170 d of the subsequent pregnancy and 2) between d 5 to 8 postpartum of the subsequent postpartum period.

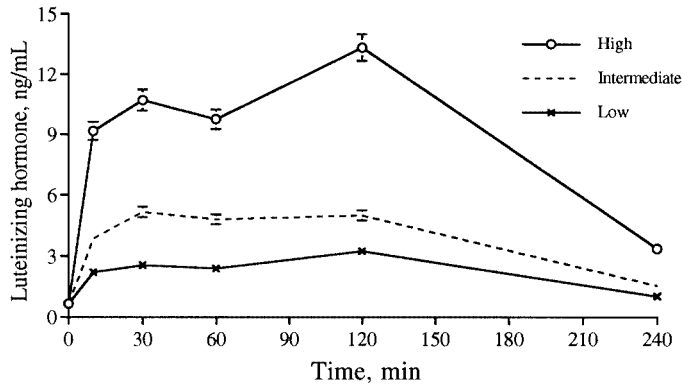


Figure 1. Anterior pituitary responses (least squares means \pm SE) to a pharmacological injection of GnRH (100 μ g, i.v.) in pluriparous cows ($n = 137$) and primiparous heifers ($n = 58$) between d 5 and 8 postpartum. Cows and heifers were classified as High (17.4%; ≥ 1 SD above the mean), Intermediate (69.2%; within 2 SD of the mean), or Low (13.3%; ≥ 1 SD below the mean) based on peak concentrations of LH after GnRH treatment. Both mean peak LH and AUC differed ($P < .001$) between each classification according to the above criteria.

Blood Collection Procedure and Hormone Analyses

Blood was collected in evacuated tubes, placed on ice for 2 h, and then allowed to clot at room temperature. Samples were centrifuged and serum was harvested for storage at -20°C until the time of analyses. Previously validated RIA were used to determine serum concentrations of estradiol-17 β (Talavera et al., 1985) and LH (McVey and Williams, 1989). Progesterone concentrations were determined with the Coat-A-Count direct assay (Diagnostic Products, Los Angeles, CA). The sensitivity of this assay averaged $.05 \pm .02$ ng/mL. Cross-reactivity of the antiserum with other related steroids was $< 1\%$. For estradiol-17 β and LH, assay sensitivities were 2.5 pg/mL and .2 ng/mL, respectively. Intraassay and interassay CV were at or below 12 and 20%, respectively, for each of the assays.

Statistical Analyses

The effects of classification type (Class I: High, Intermediate, or Low; Class II: Early or Late peak), parity,

and trial on LH release variables, including maximal LH concentration, AUC, and time to maximal LH concentration were subjected to analysis of variance using the GLM procedure of SAS (1985). Pretreatment concentrations of estradiol-17 β and LH and body condition score were used as covariates in the analyses. Correlation analyses (SAS, 1985) were performed to determine the relationship between maximal concentrations of LH and AUC after GnRH treatment. Calculation of AUC was done as reported by Akena et al. (1995). Effects of response classification (Class I or Class II), trial, parity, and response classification \times trial on PPI were determined with analysis of variance. Interclass correlations for peak LH concentrations in the subset of repeat-challenge cows were evaluated using Pearson's correlation (SAS, 1985).

Results

Anterior Pituitary Response Characteristics

Anterior pituitary responses to GnRH among the 195 cows and primiparous heifers in this study approximated a normal distribution, with 17.4 ($n = 34$), 69.2 ($n = 135$), and 13.3% ($n = 26$) classified as High, Intermediate, and Low (Class I), respectively (Figure 1, Table 1). Mean peak concentrations of LH and AUC, by definition, differed ($P < .001$) between high-, intermediate- and low-responding cows, and mean maximal LH concentrations were highly correlated ($r = .99$) with AUC. There were no Class I \times trial interactions on mean LH peak concentration or AUC.

Although mean peak concentrations of LH were similar for cows with early and late peaks (Class II), AUC was less ($P < .05$; Figure 2, Table 2) in females in which the LH peak occurred early ($n = 111$) than in females in which it occurred late ($n = 84$). More primiparous heifers (67.2%) had a maximal concentration of LH at 10 to 30 min after injection than did cows (54.7%), and 17.2% of the heifers exhibited maximal concentrations of LH at 120 min compared to 37% of the cows. The remainder of the animals had maximal concentrations of LH at 60 min after GnRH treatment. Pretreatment concentrations of LH and estradiol-17 β enhanced ($P < .001$ to $P < .04$) mean maximal concentrations of LH, AUC, time to maximal LH concentration, and PPI, but

Table 1. Peak concentrations of LH, area under the curve (AUC), and time to peak LH (least squares means \pm SE) following 100 μ g (i.v.) of GnRH administered between d 5 and 8 postpartum in beef cows classified as High, Intermediate, or Low^a

Group	n	LH peak, ng/mL	AUC	Time to peak, min
High	34	17.4 \pm .6 ^b	8.4 \pm .4 ^e	58.5 \pm 7.6
Intermediate	135	6.6 \pm .32 ^c	3.1 \pm .2 ^f	55.8 \pm 3.9
Low	26	1.9 \pm .08 ^d	1.5 \pm .5 ^g	53.6 \pm 9.5

^aPhenotypic classification based on response to 100 μ g (i.v.) of GnRH between d 5 and 8 postpartum (Low, ≥ 1 SD below the mean; Intermediate, within 1 SD of the mean; High, ≥ 1 SD above the mean).

^{b,c,d}Within columns, least squares means lacking a common superscript letter differ ($P < .01$).

^{e,f,g}Within columns, least squares means lacking a common superscript letter differ ($P < .05$).

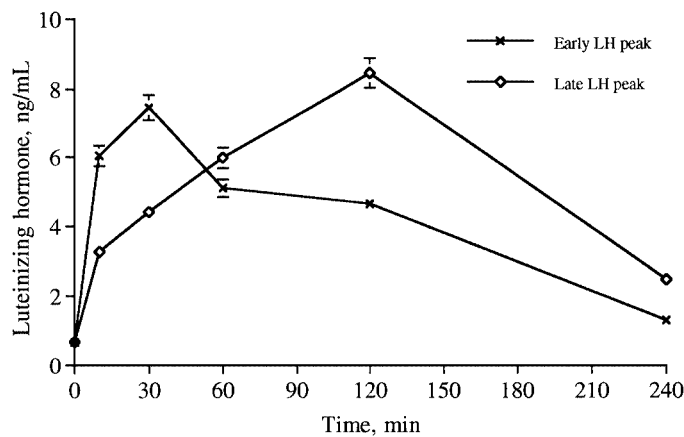


Figure 2. Least squares mean (\pm SE) concentrations of LH after 100 μ g (i.v.) of GnRH in pluriparous cows ($n = 137$) and primiparous heifers ($n = 58$) between d 5 and 8 postpartum. Animals were classified as Early ($n = 111$; 10 to 30 min) or Late ($n = 84$; 60 to 120 min) relative to time of the LH peak following treatment. Mean areas under the curves differed ($P < .05$) between the two groups.

no significant interactions were detected. Mean basal concentrations of LH ($.7 \pm .03$ ng/mL) and estradiol-17 β ($7.4 \pm .3$ pg/mL) and mean body condition score ($5.4 \pm .1$) were similar ($P > .05$) among Class I and Class II females.

In the subset of cows ($n = 18$) used to estimate repeatability of pituitary responses, pretreatment concentrations of LH did not differ ($P > .1$) between classifications, but mean maximal LH concentration and AUC were greater ($P < .002$) in the High than in the Low group during all three challenges (Figure 3). For Class II, mean time to LH peak for cows classified initially as Early or Late continued to differ ($P < .05$) at the subsequent postpartum challenge, but not at the challenge at 170 d of gestation (Figure 4). For both Classes I and II, regression of responses at challenges 2 and 3 on 1 and 3 on 2 yielded correlation coefficients from $-.21$ to $.53$, but all were generally nonsignificant ($P > .10$).

Effect of Response Classification on PPI

Of the 145 females in which luteal activity was monitored, 10 were eliminated because of spurious, uninter-

pretable values attributed to stress-induced adrenal release of progesterone. Contrasts of PPI by Class I failed to reveal consistent effects (Figure 5). However, both parity and Class II (Early or Late) affected the duration of the PPI. The pluriparous cows and cows with a late LH peak had shorter ($P < .01$ and $P < .05$, respectively) PPI than primiparous cows and cows with an early LH peak (Figure 5). Mature cows classified with a late LH peak (60 to 120 min) had the shortest PPI. There were no interactions between Class I and II variables.

Discussion

Results indicate that a sample population of beef cows at a physiologically common time point will exhibit maximum anterior pituitary responses to GnRH that are approximately normally distributed. When individual animals exhibiting phenotypically extreme responses (High vs Low) are repeatedly challenged and compared under conditions standardized as much as practically possible, mean responses for each selected subpopulation seem to remain statistically different over time. However, the individual variability associated with these responses in such a small sample ($n = 18$) were not consistent enough to yield statistically significant interclass correlations.

Postpartum intervals of cows classified as High, Intermediate, or Low did not differ. Therefore, our hypothesis that cows from an unselected population exhibiting phenotypically extreme responses (High vs Low) would exhibit consistent differences in PPI is rejected. To the contrary, classification of cows according to the timing of their temporal anterior pituitary response (Early vs Late), regardless of parity, resulted in average PPI that were 8 d shorter in the Late compared to the Early group.

The long-term aim of the experimental approaches used in this study is to identify physiological traits that can serve as indirect indicators of genetic merit for reproduction in beef cows. A basis for using anterior pituitary responsiveness to GnRH as one of those indicators is the report of Haley et al. (1989), who administered GnRH to male lambs over eight generations and selected sires on the basis of high and low responsiveness. Their approach relied not only on a physiological marker to predict reproductive merit, but also exploited the concept introduced by Land (1973) of mea-

Table 2. Peak concentrations of LH, area under the curve (AUC), and time to peak LH (least squares means \pm SE) following 100 μ g (i.v.) of GnRH administered between d 5 and 8 postpartum in beef cows classified with an Early or Late LH peak^a

Group	n	LH peak, ng/mL	AUC	Time to peak, min
Early LH peak	111	7.0 \pm .6	3.0 \pm .3 ^b	22.8 \pm 1.9 ^d
Late LH peak	84	7.8 \pm .7	4.3 \pm .4 ^c	100.7 \pm 2.3 ^e

^aPhenotypic classification based on time (10 to 30, Early; 60 to 120 min, Late) to peak LH concentration after 100 μ g (i.v.) of GnRH between d 5 and 8 postpartum.

^{b,c}Within columns, least squares means lacking a common superscript letter differ ($P < .05$).

^{d,e}Within columns, least squares means lacking a common superscript letter differ ($P < .01$).

suring traits in the male as indicators of genetic merit for reproduction in ewes. Their results indicated that, within 2 yr, a significant relationship existed between anterior pituitary responsiveness to GnRH and fecundity, particularly during the first and second breeding seasons of ewes. Importantly, age at the time of treatment of ram lambs seemed to have no effect on classification of their response (Haley et al., 1989). Moreover, the heritability of adenohypophyseal responsiveness was estimated to be moderately high ($h = .45$), providing significant opportunities for creating genetic progress.

In the current study, our approach for using a physiological marker to predict reproductive merit involved similar goals but different criteria from those used in sheep studies. Instead of measuring the trait in males,

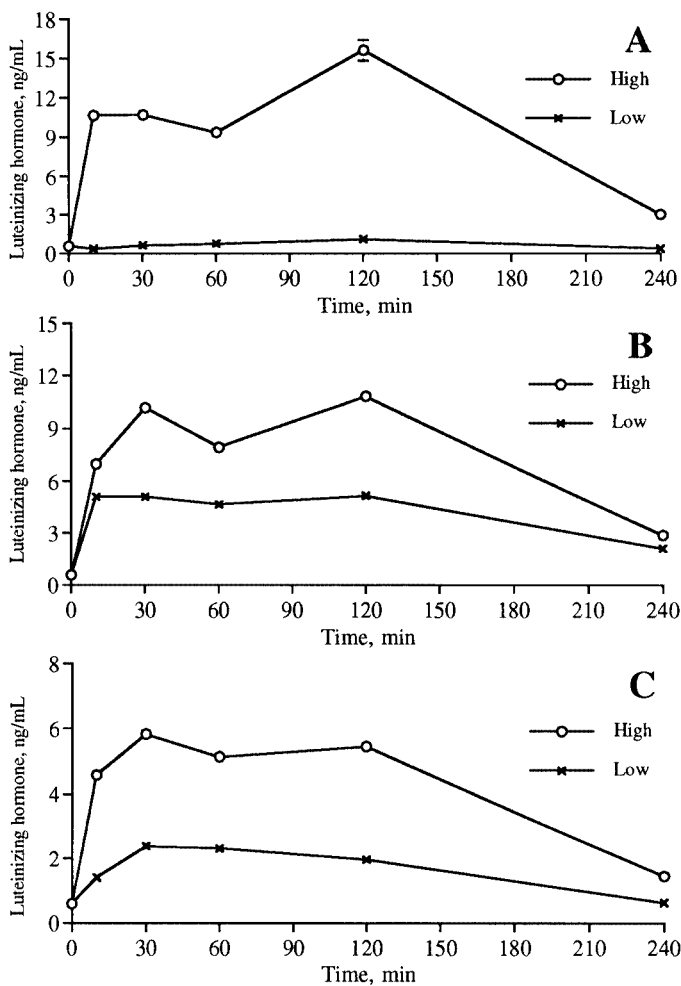


Figure 3. The GnRH-induced LH release (least squares means \pm SE) in cows classified as High ($n = 9$) or Low ($n = 9$) and treated with GnRH on two subsequent occasions. Treatment periods were A) between d 5 and 8 postpartum (initial challenge and classification), B) 150 to 170 d of gestation, and C) between d 5 and 8 postpartum in the subsequent postpartum period. Mean concentrations of LH differed ($P < .05$) during each of the three challenges; however, interclass correlations were not significant ($P > .10$).

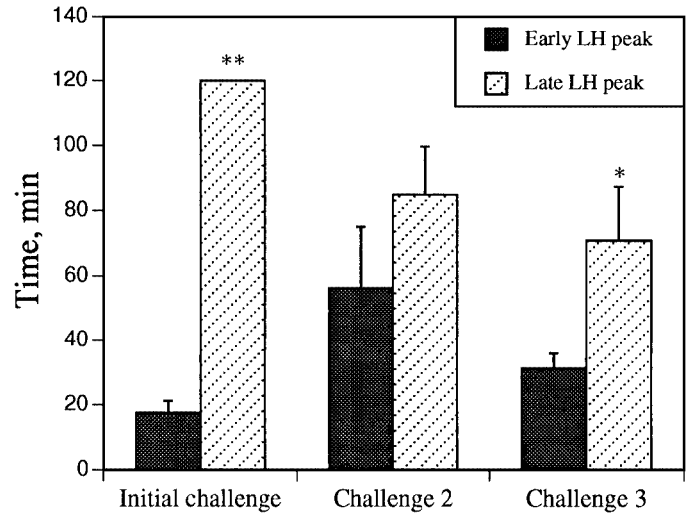


Figure 4. Time (mean \pm SEM) of peak LH release in 18 cows treated with GnRH ($100 \mu\text{g}$, i.v.) on three occasions. Cows were classified with Early (10 or 30 min; $n = 8$) or Late (60 or 120 min; $n = 10$) LH peaks during the initial challenge between d 5 and 8 postpartum. For challenges 2 and 3, means represent combined responses at 150 to 170 d of gestation and between d 5 and 8 of the subsequent postpartum period, respectively. Means with * or ** denote differences at $P < .05$ and $P < .01$, respectively. Interclass correlations were not significant ($P > .10$).

we measured it in females during a period that we believed would maximize our ability to identify phenotypically and, by inference, genotypically superior and inferior individuals. By identifying the phenotypic extremes and comparing a selected reproductive end point (PPI) between them, we theorized that a significant contrast in performance could be identified in a herd for which the trait has not been selected. Although the latter did not materialize for Class I, the identification of extreme high- and low-responding cows for use in positive assortative selection procedures (Bourdon, 1997), as opposed to simple categorization above and below the geometric mean, could conceivably accelerate the rate of subsequent genetic progress (high group) and potentiate relevant physiological and genetic contrasts for future studies.

Averaging of LH concentrations after GnRH treatment revealed that mean maximal concentrations occurred between 46 and 77 min, based on our sampling regimen. However, averaging masks the biphasic release pattern known to characterize individual hypophyseal responses to pharmacological doses of GnRH (Rippel et al., 1974; Bremner et al., 1980). This pattern is explained by the storage of LH in two pools, a readily releasable and a releasable pool (Bremner and Paulsen, 1974; Yen et al., 1974), that represent the mobilization and release of LH from near the cell surface or from deeper within the cell (Adams and Nett, 1979). Therefore, it is possible that variability between animals in the attainment of peak concentrations in the current

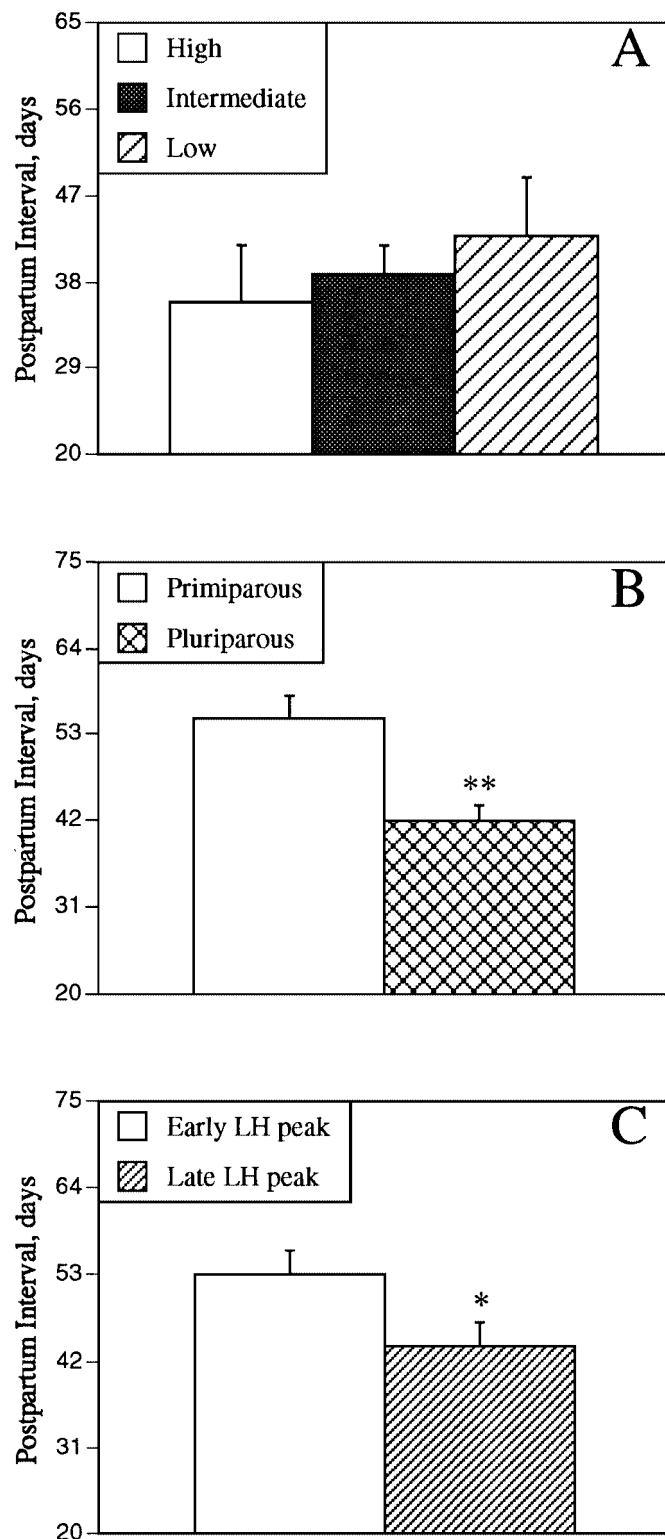


Figure 5. Mean (\pm SEM) postpartum anovulatory intervals in A) High-, Intermediate-, and Low-responding cows (Classification I), B) primiparous heifers and pluriparous cows, and C) cows exhibiting an Early or Late peak LH release (Classification II) in response to GnRH treatment. Means with * or ** denote differences at $P < .05$ and $P < .01$, respectively.

study (10 to 30 vs 60 to 120 min after injection; Class II) could have some relationship to individual variation in the conversion of nonsecretory gonadotrophs (Wise et al., 1986) and/or the partitioning of LH between readily releasable and releasable pools. Smith et al. (1986) have concluded that secretory activity of single pituitary cells is defined as much by the operational state of the receptor-release apparatus as it is by hormone content. Support for this concept has been provided in the elegant studies with sheep in which differences between High and Low line sheep have been attributed to an enhanced synthetic capacity of gonadotrophs (McNeilly et al., 1993), greater storage of LH within the gonadotrophs (Evans et al., 1995), higher amplitudes of LH pulses and mean serum concentrations of LH during the follicular phase (Evans et al., 1994), and greater numbers of hypophyseal receptors for GnRH (Evans et al., 1997).

Use of the early puerperium to examine hypophyseal responses to GnRH in the context of the current objectives has several hypothetical advantages, as previously explained. However, the model can also be complicated by several factors, including nutritional status, the existing estrogen environment, and season. Both parity and pretreatment estradiol were found to influence peak LH responses. Parity effects on LH characteristics and PPI required consideration of group comparisons within trial, and it is possible that practical use of these procedures might predicate within-year or within-season classification systems.

Implications

In unselected postpartum beef cows, the magnitudes of individual responses to GnRH approximated a normal distribution on d 5 to 8 postpartum (Class I). Temporal responses (Class II) to GnRH were significantly related to average postpartum anovulatory interval (PPI). These observations should encourage further investigations into the use of these phenomena as physiological markers for reproductive potential. For Class I, the initial identification of phenotypically high-responding cows may not be related to measurable advantages in reproductive traits (e.g., PPI). However, because of the magnitude of differences in luteinizing hormone responses for Class I and the high heritability (.45) for the trait as estimated in sheep, genetic selection could yield beneficial progress in one or more reproductive end points after several generations.

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