

PHYSIOLOGY AND MANAGEMENT OF THE POSTPARTUM SUCKLED COW FOR CONTROLLED BREEDING PROGRAMS

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Introduction

After an approximate 30-d period of uterine repair and involution, the resumption of normal postpartum ovarian cycles is regulated mainly by the rate of recovery of the hypothalamic-pituitary axis. Mechanisms controlling the re-initiation of patterns of LH secretion that are needed to support follicular development and ovulation include physiological recovery of the pituitary from effects of high circulating concentrations of estradiol produced by the placenta, nutritional status (body condition), suckling, season of calving, and genetics. The purpose of this review is to 1) summarize our understanding of mechanisms controlling the length of the postpartum anovulatory period in the suckled beef cow; and 2) consider management approaches that can exploit our understanding of postpartum physiology, nutrition and management to enhance reproductive performance.

Physiology of Postpartum Reproduction

Gestational Effects on the Hypothalamic-Pituitary Axis

Pituitary stores of LH are very low at parturition in cattle, owing to the effects of high circulating concentrations of placental-derived estradiol that are observed during late gestation (Nett, 1987). High circulating concentrations of estradiol inhibit the synthesis of the β subunit, and to some degree, the α subunit of the LH molecule in gonadotrophs. Storage and release of follicle-stimulating hormone (FSH) does not change appreciably during the postpartum period. Following parturition, the rapid decline in circulating estrogens allows a rapid re-accumulation of anterior pituitary LH, which requires 2 to 3 wk to complete. During this period of recovery, circulating concentrations of LH and frequency of LH pulses are usually low. This occurs initially because of a lack of releasable LH in all cows, regardless of whether they are suckled, nonsuckled, or milked (Silveira et al., 1993; Griffith and Williams, 1996)). That synthesis and accumulation of pituitary LH requires only a low level of GnRH stimulation accounts for the ability of the pituitary to accumulate LH during this period. After the second or third week, the pulsatile release of LH increases in weaned beef cows and milked dairy cows, resulting in the resumption of ovarian follicular development and ovulation (Carruthers et al., 1980; Williams, 1990). However, in suckled cows, the suppressive effects of suckling on hypothalamic GnRH secretion continue to prevent an increase in pulsatile LH release. Eventually, the suckled cow escapes from the effects of suckling, or is weaned, and the frequency and amplitude of GnRH pulses increases

dramatically, the frequency of LH pulses increases, and ovarian cycles resume (Williams and Griffith, 1995; Gazal et al., 1998). Although the ability of the hypothalamus to stimulate a preovulatory LH surge through estradiol positive feedback is blunted or absent immediately after calving, the normal feedback response returns within about 2 wk postcalving.

Effects of Suckling and the Maternal-Offspring Bond

For over a half century it was assumed that chronic sensory stimulation of the teat (suckling) was the primary cause of lactational anovulation in numerous species, including cattle. However, our laboratory and others have shown that somatosensory pathways within the teat and udder are unnecessary for suckling to suppress LH secretion. Neither chronic milking nor the physical presence of the calf in the absence of suckling have measurable effects on the pulsatile pattern of LH release, and neither denervation of the udder (Williams et al., 1993) nor mastectomy (Viker et al., 1993) shortens the postpartum anovulatory interval if calves remain with their dams. Additional work has clearly shown that the maternal-offspring bond is a requisite feature of postpartum Anovulation (Williams and Griffith, 1995; Griffith and Williams, 1996). Beef females forced to suckle an alien calf for up to 6 d undergo the same neuroendocrine changes that occur with weaning: a rapid increase in the frequency of LH pulses, development of a preovulatory follicle, ovulation, and the resumption of ovarian cyclicity. Formation of a selective maternal bond by the cow plus the physical interaction of the calf in the inguinal region (bunting, oral manipulation of the flank, or suckling) appear to be responsible for neural changes that create the anovulatory state (Viker et al., 1989; Williams et al., 1993; Silveira et al., 1993; Williams and Griffith, 1995). These include an increase in hypothalamic sensitivity to estradiol negative feedback and an increase in opioid tone that causes a suppression of GnRH and LH secretion for variable periods (Acosta et al., 1983). However, the time of day during which calves suckle (eg., night vs day) has no effect on length of the postpartum interval to first ovulation or conception (Gazal et al., 1999).

Genetics and Season of Calving

The resumption of the appropriate pattern of LH secretion to promote ovarian cyclicity can be affected by at least two other factors: genotype of the cow and season of calving. Purebred *Bos indicus* cattle tend to be affected more strongly by both the negative effects of suckling and undernutrition than most purebred *Bos taurus* females. Crossbreeding, either within or between species, results in greatly improved reproductive performance, including a reduction in length of the postpartum interval (Gregory, 1969). Size of the cow and lactation potential represent genotypically-driven features that also impact length of postpartum anovulation. Both of these factors increase nutritional requirements, which in turn affect reproductive performance if nutrients are limiting. In addition, the season of calving can affect the length of the postpartum anovulatory interval by 15 to 20 days or more. Although not usually considered to be seasonal breeders, cattle are affected by photoperiod to some degree. Cows bred to calve during the late summer or early fall will invariably have shorter postpartum anovulatory intervals than cows bred to calve in winter or early spring (Hansen and Hauser, 1984). However, because the calving season is often managed to coincide with maximum forage quality and quantity, herds are

more frequently managed to calve in the spring.

Nutritional Status and Body Condition

Undernutrition, particularly a deficit in dietary energy intake, is probably the most prevalent natural and man-made cause of delayed rebreeding in cattle (Randel, et al., 1990; Short et al., 1990; Williams, 1990). Moreover, the effects of undernutrition have their greatest effects when they occur during late gestation. Cows that calve in thin body condition have greatly extended intervals to first postpartum estrus and ovulation. This occurs because of a slowing of the pituitary repletion of LH after calving and heightened effects of suckling on hypothalamic GnRH secretion. As a result, LH secretion is low and the development of ovulatory follicles is delayed for periods often exceeding 100 days or more. Many experiments have been conducted showing the effects of cow body condition and postpartum nutrition on reproductive performance. Although some of the effects of low body condition at calving can be remedied by increasing feed intake after calving, this is generally not an economically-feasible approach. Therefore, the best approach is to realiment cows during the dry period after calves are weaned and before the next calving. It is during this period that the most economical gain can be achieved and during which the cow's nutrient requirements are lowest.

Dietary Fat Supplementation

For many years, we examined the potential of dietary fat supplementation to enhance reproductive performance in beef cows. The original studies on this topic were conducted in North Dakota and addressed the effects of dietary fat supplementation on circulating concentrations of progesterone in dairy heifers (Talavera et al., 1985). In that study, and in others conducted subsequent to it, fat supplementation enhanced circulating concentrations of progesterone and enhanced the lifespan of induced CL in early postpartum beef cows (Williams, 1989; Ryan et al., 1995).

Metabolic and ovarian effects. The initial studies in beef cattle were conducted with the objective of determining whether certain metabolic changes could be created to improve reproductive performance in cows in marginal to thin body condition at calving, independent of BW/BCS gain (Williams, 1989; Wehrman et al., 1991; Ryan et al., 1994; 1995). Our overriding goal was to create metabolic changes that would allow range beef cows in moderately thin condition to perform more efficiently than would be expected without such changes. It was assumed that most of these effects would occur directly at the ovarian level, without effects on the hypothalamic-pituitary axis, and for the most part, this has been confirmed. Results indicated that increasing dietary fat consumption increased the number of follicles in the medium-sized classification by 1.5- to 5-fold within 3 to 7 wk and these changes occurred coincident with changes in serum insulin, GH and intraovarian insulin-like growth factor (IGF-1) (Wehrman et al., 1991; Ryan et al., 1992; Thomas et al., 1997). All studies employed an experimental design in which treatment and control diets were isocaloric and isonitrogenous. Using this approach, it was shown unequivocally that the effects of fat supplementation did not depend upon increased dietary energy or weight gain of cattle (Wehrman et al., 1991; Thomas et al., 1997). The greatest increase in medium

follicle populations occurred in response to plant oil consumption, which as discussed below, is likely a direct result of the effects of high levels of linoleic acid in the rumen. Sources of plant oil have included whole cottonseed, soybean oil and rice bran. Unfortunately, we were not able to increase the number of ovulatory follicles in superovulation regimens using this dietary strategy (Thomas and Williams, 1996). Maximum follicular growth responses to plant oil supplementation have occurred when plant oils were fed at 4 to 6% of diet dry matter, with lesser increases noted with lower levels of added fat. Animal tallow, calcium salts of saturated fatty acids or fish oil have been shown to have less robust effects on follicular growth than plant-derived oils. Moreover, postpartum beef cows calving in very thin body condition (BCS of 3; 1-9 scale) were unable to develop medium or large follicles at a rate equal to those with a body condition score of 4 or greater after 3 wk of fat consumption (Ryan et al., 1994). Longer feeding intervals in cows in very thin condition (BCS 3) have not been examined. **Table 1** summarizes the effects of dietary fat supplementation on follicular physiology and growth as observed in our lab and in others.

Table 1. Summary of effects of dietary fat supplementation in cattle on ovarian follicular growth and steroidogenic potential of follicle cells in vitro (From Williams and Stanko, 2000 with permission)

Source	Characteristics Affected
Wehrman et al., 1991; Ryan et al., 1992; Hightshoe et al., 1991; Lucy et al., 1991; Thomas and Williams, 1996; Thomas et al., 1997; Lammoglia et al., 1996; Stanko et al., 1997; De Fries., et al., 1998	Increased number of medium-sized follicles (polyunsaturated fat > saturated and highly polyunsaturated fat effects)
Wehrman et al., 1991; Ryan et al., 1992	Increased granulosa cell progesterone production in vitro; increased follicular fluid progesterone
Ryan et al., 1992; Thomas and Williams, 1996	No effect on superovulation rate
De Fries et al., 1998	Increased number of large follicles; increased size of largest follicle

Effects on postpartum ovarian cyclicity. In early studies conducted at the Animal Reproduction Laboratory, Beeville, supplementation of postpartum, lactating beef cows with whole cottonseed beginning 30 d before the start of the breeding season increased the number of cows cycling at the start of the breeding season by up to 18% (Wehrman et al., 1991). This response was most evident when environmental conditions resulted in a loss of body condition during the postpartum period, in spite of supplementation (**Table 2**). Work at other locations has confirmed that fat supplementation reduces the postpartum anovulatory interval and may enhance rebreeding performance (**Table 3**). However, several of the latter trials were conducted with saturated or bypass fat. Therefore, we have speculated that performance would be further enhanced if polyunsaturated plant oils had been used, since ovarian responses to saturated fats appear less robust than to polyunsaturated fats.

Table 2. Effects of feeding high fat supplements to suckled, postpartum beef cows for 1 mo prior to the start of breeding on incidence of luteal activity at the start of the breeding season (From Wehrman et al., 1991 with permission)

Group ^a	Year	No. Cows	Luteal activity, %
High fat	1	61	72.0
Control	1	59	57.6
High fat	2	31	42.0
Control	2	32	18.8
High fat	Both	92	61.9 ^b
Control	Both	91	43.9 ^c

^aHigh Fat and Control supplements were isocaloric and isonitrogenous

^{b,c}Means with differing superscripts differ ($P < .05$)

Table 3. Summary of reports summarizing the positive effects of fat supplementation on postpartum reproductive performance.

Reference	Class of Cattle	Type of Fat	Response
Wehrman et al., 1991	Postpartum	Polyunsaturated	Earlier Cyclicity
Hightshoe et al., 1991	Postpartum	Saturated/Polyunsat.	Earlier Cyclicity
De Fries et al, 1998	Postpartum	Polyunsaturated	Earlier Pregnancy
Espinoza et al., 1995	Postpartum	Saturated/Polyunsat.	Earlier Cyclicity
Whitney et al., 2000	Heifers	Polyunsaturated	Earlier Pregnancy

Effects on first-service conception and cumulative pregnancy rates. Recently, in a review by Funston et al. (2005), it was implied that first-service conception rates could be substantially reduced in heifers by feeding high linoleic acid supplements (ie, soybeans, whole cottonseed; Howlett et al., 2003) or could reduce overall pregnancy rates in pasture-bred cattle (Shike et al., 2004). In one of these studies, the supplement added fat at only 2% of DM, which would be expected to have marginal effects on any variable. Examination of the Howlett paper suggested a misinterpretation, as no deficits in first-service conception rate were reported. Several other studies that were reviewed showed no effect of dietary fatty acid supplementation on these variables. In my opinion and experience, high fat supplements fed within the 4-5% of DM limit present no potential for adversely affecting reproduction. This includes the feeding of whole cottonseed which contains some gossypol. This subject has been exhaustively evaluated and discounted as a concern in the vast majority of beef cattle supplementation regimes (Gray et al., 1993; Jones et al., 1991).

Table 4 summarizes a trial at Beeville involving 199, Brahman x Hereford, F₁ females (87 pluriparous cows; 53 primiparous and 59 nulliparous heifers) fed either a high fat (3.5 lb whole cottonseed) or an isocaloric/isonitrogenous, corn/cottonseed meal-based control supplement beginning 30 d before the start of the breeding season and continuing for 30 d into the breeding season. Heifers were 14-15 months of age and averaged 725 lb (329.5 kg). All cattle had a BCS of at least 5 (5.2 ± 0.4). Females were stratified by age, parity, date of calving and BCS and allocated randomly to a 2 x 2 factorial arrangement of treatments: 1) Control-Normal Fat, 2) Control, High Fat 3) SMB, Normal Fat and 4) SMB,

High Fat. Synchronized females (SMB-treated) received the standard 9-day SMB regimen, and calves were removed from all cows for 48 h at the time of SMB implant removal. All SMB females were inseminated by TAI at 48-54 h after implant removal (SMB) and females in all groups were placed with fertile bulls 5 d after TAI in the SMB groups. Results indicated no beneficial or detrimental effects of fat supplementation on TAI conception rates or 45-day cumulative pregnancy rates. However, there was a tendency for fewer synchronized cows to be pregnant on d 45 than non-synchronized.

Table 4. Effects of SMB synchronization and high fat supplementation on TAI conception and cumulative 45-day pregnancy rates in Brahman x Hereford, F₁ females

Group	Age	No.	TAI conception, %	45-Day Pregnancy, %
SMB-Normal Fat	Pluriparous	22	54.5	82.0
	Primiparous	13	46.1	78.6
	Nulliparous	15	47.0	100
	Total	50	50.0	86.3
SMB-High Fat	Pluriparous	22	50.0	81.8
	Primiparous	14	42.8	92.8
	Nulliparous	15	53.3	80
	Total	51	49.0	84.3
Control-Normal Fat	Pluriparous	22	N/A	100
	Primiparous	13	N/A	100
	Nulliparous	14	N/A	92.8
	Total	49	N/A	97.9
Control-High Fat	Pluriparous	21	N/A	95.2
	Primiparous	13	N/A	92.3
	Nulliparous	15	N/A	92.8
	Total	49	N/A	93.8

Fat supplementation and onset of puberty. Several studies have examined the effects of high fat diets on age at puberty. Because sexual maturation is a brain-mediated event, we have no basis to expect and have not observed any effect of fat supplementation on age at puberty in *Bos indicus* x *Bos taurus* heifers (Garcia et al., 2003). A review of published studies in heifers by Funston et al. (2004) generally confirms this view, although one or two studies have shown small effects on reducing age at puberty.

Effects on uterine prostaglandin release. In addition to the studies summarized above that have examined the effects of dietary fat intake on lipoprotein cholesterol metabolism, insulin, growth hormone, and IGF-1 secretion, and ovarian follicular growth, other laboratories have focused on the role of fat supplementation and fatty acid metabolism on prostaglandin synthesis by the uterus. The primary basis of this work relates to the desire to modulate uterine prostaglandin synthesis during early pregnancy so as to avoid premature

luteal regression. This information is reviewed in more detail elsewhere (Staples et al., 1998; Thatcher and Staples, 2000). However, suffice it to say in the context of this overview that no definitive studies have been published to demonstrate that supplemental fats high in linoleic acid or in the n-3 fatty acids found in fish oil can consistently improve or diminish reproductive performance of beef or dairy cattle.

Management of Postpartum Reproduction

Selection for Fertility

Heritability of reproductive traits has traditionally been considered low, making genetic progress for reproductive efficiency slow. However, much of this lack of robustness is caused by environmental x genotypic interactions which make it difficult to accurately assess genetic worth. As already stated, crossbreeding has a large positive effect on reproductive efficiency. The use of physiological or genetic markers for reproduction has begun to be examined for their value in identifying superior individuals early in their life. One approach used at the Animal Reproduction Laboratory in Beeville was to examine responsiveness of the pituitary to GnRH early after calving (days 5-8 postpartum) and in heifers during pubertal development (Fajersson et al., 1999). We found that great variability exists in pituitary responsiveness to GnRH, forming essentially a normal distribution. In this herd, which has been selected for fertility, cows with high responses to GnRH did not have postpartum anovulatory intervals different from low-responding cows. However, cows exhibiting an early LH peak after a pharmacological challenge with GnRH had a longer postpartum interval than those with a late peak. The same measures in heifers did not predict age at puberty. Nevertheless, further work is needed in these areas, as the heritability for pituitary responsiveness to the gonadotropins has been shown to be near 0.45 in sheep. It is assumed that, in the future, it will be more likely that genotypic markers will be used for the selection of superior traits rather than physiological markers. Unfortunately, reproduction is a complex trait controlled by many genes. Therefore, identifying and selecting for increased frequency of a single gene may result in changes in products of that gene without improving overall reproductive performance.

Body Condition and Postpartum Reproduction

Body condition scoring (BCS) is an important element in management of beef cattle. On a 1 to 9 scale (1 = emaciated; 9 = obese), it is desirable to maintain cows in at least a BCS of 5 (good condition). However, cattle are managed throughout the world in environments that often result in BCS falling below this recommended level, and economics may not allow its prevention by supplemental feeding. Therefore, if BCS is allowed to vary with changes in environment and forage availability, attempts should be made through management to achieve a BCS as high as possible before calving. A low BCS at calving has greater negative effects than losses in BCS after calving or after conception (Short et al., 1990; Randel et al., 1990). If cows calve in excellent to moderate (BCS 5-6) condition, they can often rebreed early enough to withstand nutritional challenges during lactation. Therefore, they should be managed to recover body condition during the dry period and before the next parturition. Alternatively, positive effects on reproductive performance can

be realized if cows calving in less than optimum BCS are fed to gain body weight and condition after calving. However, **this is not a very economical approach** as significant amounts of supplemental nutrients will be used for milk production as opposed to reproduction. Therefore, it is best to calve cows in good body condition and then use strategic supplementation with protein to enhance intake and digestion of low to medium-quality forages for maintaining body condition.

Practical Supplementation Strategies Using Fat: Claims and Controversy

Fat supplementation and postpartum reproductive performance. As is the case for any technology or management strategy that improves specific aspects of ovarian physiology and cyclic activity, actual improvements in pregnancy rates, weaned calf crop, or total kg of calf produced is dependent upon an array of interactive management practices and environmental conditions. No studies have been conducted demonstrating that long-term use of fat supplementation during the postpartum, rebreeding period will contribute to markedly improved pregnancy rates or enhanced economic outcome. The majority of field studies that have examined the effects of fat supplementation on reproductive performance have suffered from the use of small numbers of animals, feeding strategies (e.g., prepartum; Bellows et al., 2001) that failed to appropriately exploit the physiological basis for fat supplementation established in earlier studies, or used cattle whose reproductive performance would not be expected to be compromised. Therefore, although a host of important physiological responses to fat supplementation have been documented, optimal strategies that provide predictable and consistent enhancements to reproductive performance have not been developed.

Feeding ruminant animals excessive quantities of fat (> 5% of total dry matter intake) can result in a marked negative effect on fiber digestibility and on dry matter intake. This occurs because of selection against microorganisms with cellulolytic capability. The level of fat that can be fed is also dependent upon the form of the feedstuff from which it is derived, and 5% of total dry matter may not be the maximum tolerable amount under all conditions. Fat contained in whole oilseeds can be fed at much higher levels than free oils mixed throughout the diet, as the oil is released into the rumen more slowly. Due to the lack of reactive double bonds, saturated fatty acids, such as those that predominate in animal tallow, pass through the rumen undegraded and are considered bypass fats. Some of the effects that these bypass fats have on the metabolism and physiology of the animal are potentially quite different from those created by polyunsaturated fatty acids metabolized in the rumen, although their caloric values are similar.

Sources of fat. The majority of the early work studying fat supplementation effects on reproduction employed either whole oilseeds, soybean oil, or Megalac®, which contains calcium salts of palm oil. Depending upon oil content, oilseeds were fed at a rate of 15 to 30% of the diet on a dry matter basis, and supplied 4 to 6% added fat. Oilseeds, particularly cottonseed, provide a unique blend of energy, protein, fiber, and fat and make an excellent supplemental feed when fed at 0.9 to 2.2 kg per head daily. An issue that has been raised regarding the use of whole cottonseed is that of gossypol toxicity. Beef cows consuming up to 20 g daily of dietary free gossypol for up to 2 months, via diets containing direct solvent-

extracted cottonseed meal (high gossypol) and whole cottonseed, exhibited no effects on reproductive endocrine function, estrous cycles, or pregnancy rates (Gray et al., 1993). Although high levels of gossypol do produce increased red blood cell fragility, this effect does not appear to create a clinically-significant pathology in beef cows under normal management conditions. Moreover, the levels of gossypol present in typically fed quantities of whole cottonseed for protein or fat supplementation (as described above) provided only a fraction of the amount of gossypol fed in the studies summarized above. In mature female cattle, the only reports of gossypol toxicity have been in the dairy industry involving diets containing up to 45% direct solvent cottonseed meal for 14 weeks. The reader is referred to a complete treatise on the subject of gossypol-containing feeds and gossypol toxicity in beef cattle (Jones et al, 1991).

Oilseeds are not universally available or economically practical under all conditions in which beef cattle supplementation is employed. Therefore, other alternatives are needed. One of these alternatives is molasses-based liquid supplements containing soybean oil soapstocks. Technology to maintain fat in a homogenous suspension for long periods continues to be the major challenge, and optimization of blends containing urea, sugars, fat and other constituents to promote consistent intake will be required. Recently, dry fat supplements containing 18 to 20% plant oil have been marketed for grazing beef (CONCEPT; Purina Mills, St. Louis, MO) and dairy cattle (High Fat Product; ADM, Decatur, IL) to exploit the benefits of fat supplementation on reproductive performance. Animal tallow has been used in supplements designed to enhance reproductive performance; however, there are marked palatability problems associated with high feedstuff concentrations of tallow. Therefore, it appears that plant-derived oils, when recommended for use at levels shown to maximize ovarian physiological responses, will continue to be the source of choice. Alternative commercial supplements or other by-products containing up to 20% plant oils are needed. Yellow grease, a by-product of the restaurant trade (20 to 25% linoleic acid), can be used as one of those alternatives.

Suckling Management

An increased understanding of how suckling mediates its negative effects on postpartum reproduction has aided our attempts to develop management protocols to reduce those effects. The following is a list of procedures that have been utilized to obviate the effects of suckling.

1. Temporary Calf Removal. This practice has been used since the early 1970's, particularly in association with estrous synchronization protocols. For example, removal of calves for 48 hours beginning at the time of removal of a progestin implant (SYNCRO-MATE-B; CRESTAR) or after GnRH treatment (OvSynch) will improve synchrony and timed-AI conception rates. However, we do not recommend that 48-hour calf removal be used alone to stimulate ovulation in anovulatory cows. In our experience, 48-hour calf removal is inadequate to achieve ovulation in more than 30% of anovulatory cows. This occurs because many cows that are responding to calf removal will again be suppressed by suckling if the calf is returned at 48 h (Williams et al., 1995). Moreover, this first ovulation is often not accompanied by

- estrus. As it is not prudent to leave calves off of cows for more than 48 h due to health considerations, we recommend 48-h calf removal only when it can be combined with synchronization treatments that tend to induce ovulation in anovulatory cows.
2. Early Weaning. This technique is used in the U.S. when it is more economical to feed the calf than it is to feed the lactating cow. It is usually reserved for severe drought conditions and can allow managers to rebreed their cows without the high nutrient requirements associated with lactation.
 3. Once-Daily Suckling. This is also a tool that is beneficial, particularly with first-calf heifers, when environmental conditions are challenging. First-calf, grazing heifers have been shown to return to estrus at a dramatically earlier rate than heifers suckled *ad libitum* (Randel, 1981).
 4. Alien Suckling. As reviewed above, we now know that the maternal bond between a cow and her suckling calf is an important element in suckling-mediated anovulation. However, if cows are forced to suckle an alien for up to 6 d, cows will be “physiologically weaned” and ovarian cycles will resume. In the U.S., there are few if any management systems in which this tactic is practical. However, in countries in which cattle are managed for dual purposes (eg, milk and beef production), the use of alien suckling could prove beneficial and practical. Using this system, small groups of cows are usually intensively managed on a daily basis for both milking and suckling by the calf. Therefore, it should be possible to temporarily replace the cow’s own calf with an alien for approximately 1 wk under controlled suckling conditions. This will result in the induction of ovulation in anovulatory cows, continue to allow milking of the cow, and provide adequate milk for the alien during the 6-day period. However, we have observed that suckled, Brahman-influenced cows tend to resist milk let-down when suckled by an alien; therefore, these calves often obtain milk only from the cisternae. As a result, total milk production is likely to decline during the 6-d alien suckling period.
 5. Alien Cohabitation. This is a modification of the system described above and has been implemented successfully in estrous synchronization protocols. Since alien suckling does not have negative effects on LH secretion, we hypothesized that cohabitating alien or unrelated calves with cows during synchronization could substitute for 48-h calf removal and perhaps benefit the husbandry of calves weaned from their own dams. In those experiments, approximately 30% of Brahman x Hereford, F₁ females allowed some degree of suckling by an alien calf when housed in pens together with alien calves. Total suckling time by these calves over the 48-h period averaged 14.7 to 24 min, and the proportion of calves attempting suckling ranged from 24 to 44%. Alien suckling did not reduce calf weight losses compared to weaned calves. However, timed AI conception rates in cows treated with SMB were equal for cows subjected to 48-h weaning and alien cohabitation, but greater than cows allowed to suckle their own calves *ad libitum*.

Summary and Conclusions

An extended and variable period of anovulation occurs in suckled beef cows after parturition. This phenomenon exerts both biological and economic limitations on the efficiency of beef production world-wide. Intensive research efforts over the last 40 years have identified factors that regulate the length of the postpartum anovulatory interval, including post-gestational recovery of the hypothalamic-pituitary axis, nutrition, suckling, season of calving, and genotype. Moreover, a detailed understanding of many of the physiological, cellular, and molecular mechanisms underlying these effects has evolved and has, in some cases, yielded enlightened approaches to cattle management. Increased consumption of dietary fat influences ovarian follicular growth, steroid hormone production, growth factor synthesis or accumulation in follicular fluid, luteal activity, and postpartum anovulatory intervals in cattle. However, methods to consistently improve rebreeding performance have not been demonstrated. Major challenges remain in our efforts to link increased scientific understanding with management strategies and biotechnologies that are economically relevant.

Literature Cited

- Acosta, B., T. E. Tarnavsky, T. E. Platt, D. L. Hamernick, J. L. Brown, H. M. Schoenmann, and J. J. Reeves. 1983. Nursing enhances the negative effect of estrogen on LH release in the cow. *J. Anim. Sci.* 57: 1530-1536.
- Bellows, R. A., E. E. Grings, D. D. Simms, T. W. Geary, and J. W. Bergman. 2001. Effects of feeding supplemental fat during gestation to first-calf beef heifers. *Prof. Anim. Sci.* 17:81-89.
- Carruthers, T. D., E. M. Convey, J. S. Kesner, H. D. Hafs, and K. W. Cheng. 1980. The hypothalamo-pituitary-gonadotropic axis of suckled and non-suckled dairy cows postpartum. *J. Anim. Sci.* 51: 919-925.
- De Fries, C. A., D. A. Neuendorff, and R. D. Randel. 1998. Fat supplementation influences postpartum reproductive performance in Brahman cows. *J. Anim. Sci.* 76:864-870.
- Fajersson P., R. L. Stanko, and G. L. Williams. 1999. Distribution and repeatability of anterior pituitary responses to GnRH and relationship of response classification to the postpartum anovulatory interval of beef cows. *J. Anim. Sci.* 77:3043-3049
- Funston, R.N. 2004. Fat supplementation and reproduction in beef females. *J. Anim. Sci.* 82(E. Suppl.):E154-E161
- Funston, R. N. 2005. Nutrition and Reproduction Interactions. In Proceedings, Applied Reproductive Strategies in Beef Cows, Texas A&M University, College Station (in press)
- Gazal, O. S., G. A. Guzman Vega, and G. L. Williams. 1999. Effects of time of suckling during the solar day on length of the postpartum anovulatory interval in Brahman x Hereford (F₁) cows. *J. Anim. Sci.* 77: 1044-1047
- Gazal, O.S., L.S. Leshin, R.L. Stanko, L. L. Anderson, and G.L. Williams. 1998. Pulsatile release of gonadotropin-releasing hormone into third ventricle cerebrospinal fluid of cattle: Correspondence with the tonic and surge release of luteinizing hormone and its tonic inhibition by suckling and neuropeptide Y. *Biol Reprod.* 59: 676-683
- Garcia, M. R., M. Amstalden, R. L. Stanko, C. D. Morrison, D. H. Keisler, and G. L. Williams. 2003. Age at puberty, total fat and conjugated linoleic acid content of

- carcass, and circulating metabolic hormones in beef heifers fed a diet high in linoleic acid beginning at four months of age. *J. Anim. Sci.* 89: 261-268
- Gray, M. L., L. W. Greene, and G. L. Williams. 1993. Effects of dietary gossypol consumption on metabolic homeostasis and reproductive endocrine function in beef heifers and cows. *J. Anim. Sci.* 71: 3052-3059
- Gregory, K. E., 1969. Principles of Beef Cattle Breeding. P. 45-89 in *Beef Cattle*, 6th ed. John Wiley and Sons, Inc., New York.
- Griffith, M. K. and G. L. Williams. 1996. Contribution of maternal vision and olfaction to suckling-mediated inhibition of LH secretion, the expression of maternal selectivity, and lactation in beef cows. *Biol. Reprod.* 54:761-768.
- Hansen, P. J. and E. R. Hauser. 1984. Photoperiod alteration of postpartum reproductive function in suckled cows. *Theriogenology* 22: 1-14.
- Hightshoe, R. B., R. C. Cochran, L. R. Corah, G. H. Kiracofe, D. L. Harmon, and R. C. Perry. 1991. Effects of calcium soaps of fatty acids on postpartum reproductive function in beef cows. *J. Anim. Sci.* 69: 4097-4103.
- Howlett, C. M., E. S. Vanzant, L. H. Anderson, W. R. Burris, B. G. Fieser, and R. F. Bapst. 2003. Effect of supplemental nutrient source on heifer growth and reproductive performance, and on utilization of corn silage-based diets by beef steers. *J. Anim. Sci.* 81:2367-2378.
- Jones, L.A., D. H. Kinard and J. S. Mills (eds), 1991. *Cattle Research with Gossypol-Containing Feeds* Natl. Cottonseed Products Association, Memphis, TN.
- Lammoglia, M. A., S. T. Willard, J. R. Oldham, and R. D. Randel. 1996. Effects of dietary fat and season on steroid hormonal profiles before parturition and on hormonal , cholesterol, triglycerides, follicular patterns and postpartum reproduction in Brahman cows. *J. Anim. Sci.* 74: 2253-2262.
- Lucy, M. C., C. R. Staples, F. M. Michel, and W. W. Thatcher. 1991. Effect of feeding calcium soaps to early postpartum dairy cows on plasma prostaglandin $F_{2\alpha}$, Luteinizing hormone, and follicular growth. *J. Dairy Sci.* 74: 483-489.
- Nett, T. M. 1987. Function of the hypothalamic-hypophyseal axis during the postpartum period in ewes and cows. *J. Reprod. Fert. Suppl.* 34: 201-213.
- Randel., R. D. 1981. Effect of once-daily suckling on postpartum interval and cow-calf performance of first calf Brahman x Hereford heifers. *J. Anim. Sci.* 53; 755-757.
- Randel R.D. Nutrition and postpartum rebreeding in cattle. *J Anim Sci* 1990; 68:853-862.
- Ryan, D. P., R. A. Spoon, M. K. Griffith, and G. L. Williams. 1994. Ovarian follicular recruitment, granulosa cell steroidogenic potential, and growth hormone/insulin-like growth factor-1 relationships in beef cows consuming high lipid diets: Effects of graded differences in body condition maintained during the puerperium. *Dom. Anim. Endocrinol.* 11: 161-174
- Ryan, D. P., R. A. Spoon, and G. L. Williams. 1992. Ovarian follicular characteristics, embryo recovery and embryo viability in heifers fed high fat diets and treated with follicle stimulating hormone. *J. Anim. Sci.* 70: 3505-3513
- Ryan, D. P., B. Bao, M. K. Griffith, and G. L. Williams. 1995. Metabolic and luteal sequelae to heightened dietary fat intake in postpartum beef cows. *J. Anim. Sci* 73:2086-2093
- Short, R. E., R. A. Bellows, R. B. Staigmiller, J. G. Berardinelli and E. E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle.

- J. Anim. Sci. 68: 799-816.
- Shike, D.W., D.B. Faulkner, and J.M. Dahlquist. 2004. Influence of limit-fed dry corn gluten feed and distillers dried grains with solubles on performance, lactation, and reproduction of beef cows. Proc. Midwestern Section ASAS (Abstr. 277).
- Silveira, P. A., R. A. Spoon, D. P. Ryan, and G. L. Williams. 1993. Maternal behavior as a requisite link in suckling-mediated anovulation in cows. Biol. Reprod. 49:1338-1346.
- Staples, C. R., J. M. Burke, and W. W. Thatcher. 1998. Influence of supplemental fats on reproductive tissues and performance of lactating cows. J. Dairy Sci. 81:856-871
- Talavera, F., C. S. Park, and G. L. Williams. 1985. Relationships among dietary lipid intake, serum cholesterol and ovarian function in Holstein heifers. J. Anim. Sci. 60: 1045-1051
- Thatcher, W. W., and C. R. Staples. 2000. Effects of dietary fat supplementation on reproduction in lactating dairy cows. Adv. Dairy Technol. 12:213-232
- Thomas, M. L., B. Bao, and G. L. Williams. 1996. Dietary fats varying in their fatty acid composition differentially influence follicular growth in cows fed isoenergetic diets. J. Anim. Sci. 75: 2512-2519.
- Wehrman ME, Welsh, Jr. TH, Williams GL. 1991. Diet-induced hyperlipidemia in cattle modifies the intrafollicular cholesterol environment, modulates ovarian follicular dynamics and hastens the onset of postpartum luteal activity. 1995. Biol. Reprod. 45: 514-522.
- Williams, G. L. 1989. Modulation of luteal activity in postpartum beef cows through changes in dietary lipid. J. Anim. Sci. 67: 785-793
- Williams GL. Suckling as a regulator of postpartum rebreeding in cattle: A Review. 1990. J. Anim. Sci. 68: 831-852.
- Williams G. L. and M. K. Griffith. 1995. Sensory and behavioral control of suckling-mediated anovulation in cows. In: C.D. Nancarrow and R. J. Scaramuzzi, (eds.), Reproduction in Domestic Ruminants III, J. Reprod. Fert. Suppl. 49:463-475; The Dorsett Press, Dorchester, Dorset, UK.
- Williams GL, Gazal OS, Guzman Vega GA, and Stanko RL. 1995. Mechanisms regulating suckling-mediated anovulation in the cow. In: G. M. Stone and G. Evans, (eds.), Animal Reproduction: Research and Practice, Anim Reprod Sci Suppl; 42:289-29; Elsevier Science B.V., Amsterdam.
- Williams GL. Fat, Follicles, and Fecundity: The Ruminant Paradigm. In: W. Hansel and G. Bray (Eds.), Nutrition and Reproduction: 1998;163-179; Pennington Biomed Res Found, Louisiana State Univ. Press, Baton Rouge.
- Williams, G. L., W. R. McVey, Jr., and J. F. Hunter. 1993. Mammary somatosensory pathways are not required for suckling-mediated inhibition of luteinizing hormone secretion and ovulation in cows. Biol Reprod. 49: 1328-1346
- Williams GL, Stanko RL. Dietary fats as reproductive nutraceuticals in cattle. Proc Amer Soc Anim Sci. 2000., <http://www.asas.org/jas/symposia/proceedings/0915.pdf>.
- Viker, S. D., W. J. McGuire, J. M. Wright, K. B. Beeman and G. H. Kiracofe. 1989. Cow-calf association delays postpartum ovulation in mastectomized cows. Theriogenology 32: 467-474.
- Viker, S. D., R. L. Larson, G. H. Kiracofe, R. E. Steward and J. S. Stevenson. 1993. Prolonged postpartum Anovulation in mastectomized cows requires tactile stimulation by the calf. J. Animal. Sci. 71: 999-1003.