

# Energy Intake Regulates Ovarian Function in Beef Cattle<sup>1</sup>

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## Abstract

Nutrient intake and body energy reserves are major regulators of reproductive performance of beef cows. Reduced body weight causes cessation of estrous cycles, and inadequate body energy stores at parturition prolong the postpartum anestrous interval. Nutritionally induced reduction in follicular growth is a result of decreased secretion of GnRH and LH. During anestrus, ovarian follicular waves are recurrent, but inadequate estradiol is secreted by the dominant follicle to cause estrus and ovulation. Realimentation of nutritionally induced anovulatory cows results in larger dominant follicles and ovulation occurs when body energy stores are adequate. Increased follicular growth rate is associated with increased concentrations of LH, estradiol, and IGF-I in plasma. When nutritionally induced anovulatory cows are realimented, ovulation and a corpus luteum with shorter than normal function occurs, usually without estrus, before the first normal estrous cycle. In addition, exogenous GnRH infusion induces ovulation in nutritionally induced anestrous cows. We conclude that prolonged restriction of nutrient intake reduces secretion of LH and IGF-I, less estradiol is produced by the dominant follicle, and ovulation ceases. Realimentation of anestrous animals alters metabolic signals, resulting in pulsatile LH secretion, increased size of the dominant follicle, and ovulation.

*Key Words: Nutrition, Ovary, Ovulation, Reproduction*

## Introduction

Reproductive efficiency is a major determinant of profitability in beef production. The goal of one calf annually per cow is not often achieved because too many cows do not become pregnant during the breeding season (Bellows et al., 1979). A major reason for this is inadequate nutrient intake and the resultant anestrus. Indeed, reduced energy intake increases the interval from calving to conception (Wiltbank et al., 1964; Dunn et al., 1969; Spitzer et al., 1995) and delays puberty (Ferrel, 1982; Kinder et al., 1994; Yelich et al., 1995).

When nutrient intake is greater than that required for maintenance and production, excessive energy is stored as body fat. Body energy stores can be estimated by use of a body condition scoring system (BCS; Wagner et al., 1988). Body condition scores are useful for predicting reproductive performance. A cow's BCS at calving in the spring is a major factor determining whether the cow will become pregnant during the breeding season and the interval from calving to estrus (Wiltbank et al., 1962; Richards et al., 1986; Selk et al., 1988; Randel et al., 1990; Short et al., 1990).

Suckling also regulates the interval from calving to first estrus (Williams, 1990). A variety of approaches have been used to eliminate the influence of suckling so that the effects of nutrition on reproduction can be evaluated. Restriction of energy intake of nonlactating cows or heifers with normal estrous cycles is a good model because of the well-documented suppression of reproductive function. This approach allows identification of somatically derived signals in underfed animals that might affect the hypothalamic-pituitary-ovarian axis. The purpose of this review is to describe the effect of energy intake on ovarian function of beef

cows and to evaluate potential metabolic signals involved in regulation of follicular growth.

## Discussion

### *Nutritional Effects on Pubertal Ovarian Function*

Growth rate before puberty influences age and weight of heifers at puberty. Heifers that gain at a greater rate are younger and heavier at puberty than heifers fed a lesser amount of energy (Yelich et al., 1995). Heifers with greater dietary intake had larger dominant follicles at a younger age than heifers fed diets with less energy; however, growth rate of the dominant follicle and size of the ovulatory follicle at puberty were not influenced by nutrient intake (Bergfeld et al., 1994). Well-fed prepubertal heifers had greater concentrations of estradiol in plasma than underfed heifers (Bergfeld et al., 1994). Heifers with reduced dietary intake after puberty had smaller dominant follicles, and persistence of dominant follicles was reduced (Murphy et al., 1991).

### *Nutritional Effects on Postpartum Ovarian Function*

Nutrient intake before and after parturition influences the interval from calving to first ovulation (Spitzer et al., 1995). Growth of follicles after calving is also influenced by energy intake. Body condition score of cows at calving influenced the number of medium and large ( $\geq 10$  mm) follicles at 5 to 17 d postpartum (Ryan et al., 1994). Obese cows (BCS 8) had more medium follicles at 5 d postpartum than cows with BCS of 3 (very thin), 4 (thin), or 6 (optimal), and BCS 8 cows had more large follicles at 9 d postpartum than cows with BCS of 3 or 4. At 17 d postpartum, very thin cows had fewer medium and large follicles than cows with BCS of 4, 6,

or 8. Reduced energy intake in postpartum beef cows reduced the size of dominant follicles and the number of large estrogen-active follicles and increased the persistence of small subordinates (Perry et al., 1991). Negative energy balance in postpartum dairy cows was associated with an increased number of medium-sized follicles and decreased maximum diameter of dominant follicles, whereas positive energy balance was associated with increased maximum diameter of dominant follicles and reduced growth of subordinates (Lucy et al., 1991).

### ***Nutritionally Induced Anestrus***

Restriction of nutrient intake of cows with good body condition results in loss of body weight and BCS. Normal estrous cycles and ovulation cease after sufficient weight loss occurs. Anovulation occurred in mature Hereford cows when they had lost 24% of their body weight and 36% of their BCS in 26 wk (Richards et al., 1989). Loss of 22% of the body weight of Hereford  $\times$  Angus (Bossis et al., 1999) and Brahman heifers (Rhodes et al., 1995) resulted in the cessation of estrous cycles. The onset of anestrus was associated with decreased BCS.

Realimentation of nutritionally induced anovulatory cows resulted in the resumption of estrous cycles; however, cows did not reinitiate cycles until BCS was greater than that at which cycles ceased (Richards et al., 1989). When nutritionally induced anestrus heifers were realimented with moderate nutrient intake, ovulation occurred in approximately 8 wk, when heifers had gained about 30% of their weight at anovulation (Rhodes et al., 1995; Bossis et al., 1999).

### ***Follicular Characteristics During Nutritionally Induced Anovulation***

By the early 1960s it had become apparent that follicular growth in cattle occurred in waves (Rajakoski, 1960). Follicular recruitment, selection, and dominance are the main stages of follicular growth. Several follicles begin growing, and a dominant follicle becomes larger than subordinate follicles. During the estrous cycle, one or two dominant anovulatory follicles develop before the ovulatory follicle, resulting in two or three waves in most cases (for review see Ginther et al., 1996; Roche et al., 1998). Nutritional restriction of heifers that is sufficient to cause weight loss and anovulation will result in alterations in follicular growth. We found that the day of emergence of the ovulatory follicle in heifers that lost weight during the two cycles preceding anovulation was similar to that in heifers that maintained weight (Bossis et al., 1999). Heifers that maintained weight had larger ( $P < .0001$ ) ovulatory follicles ( $15.7 \pm .9$  mm) than restricted heifers ( $10.4 \pm .9$  mm) during the last two cycles before anovulation. Growth rate of the ovulatory follicle was greater for heifers maintaining weight than for heifers on restricted diets during the two cycles before anovulation. Growth rate and diameter of the ovulatory follicle were similar during the second wave of the last two cycles before anovulation. Rhodes et al. (1995) found that the number of

dominant follicles per estrous cycle was not altered when Brahman heifers were fed restricted diets to induce anovulation. However, for each 10-kg decrease in weight the ovulatory follicle diameter decreased by  $.31 \pm .006$  mm and size and persistence of the first dominant follicle also decreased. Stagg et al. (1995a) also found that rate of growth and maximum size of the dominant follicle were less in nutritionally induced anestrus heifers than during previous ovulatory cycles. Size of corpora lutea during the two estrous cycles before the onset of nutritionally induced anestrus was reduced relative to that in heifers fed diets to maintain growth (Rhodes et al., 1995; Bossis et al., 1999).

### ***Follicular Growth During Realimentation of Nutritionally Anestrus Heifers***

Follicular waves occur during nutritionally induced anestrus of beef heifers. Follicular growth was measured in one follicular wave before realimentation (**Wan**) of anestrus heifers and in two waves (**W-2**, **W-1**) immediately before the first wave that resulted in ovulation or luteinization (**WO**) and during WO. Maximum diameter of the dominant follicle increased between anovulation and resumption of ovulation (Table 1). Growth rate of the dominant follicle increased linearly with waves before ovulation. Duration of the growing phase and regression rate of the dominant follicle also increased with waves during realimentation, and the dominant follicle was more persistent during the last two waves before ovulation compared with Wan. Growth rate of the largest subordinate follicle increased during realimentation (.8, 1.2, 1.4, and 1.7 mm/d for Wan, W-2, W-1, and WO, respectively). Maximum diameter of the largest subordinate follicle was smaller before realimentation than during the three waves preceding ovulation. Nine of 11 heifers ovulated, and two developed luteinized follicles at WO. The nine heifers that ovulated had a  $10.5 \pm .9$  d interovulatory interval, and the other two heifers ovulated 9 and 10 d after the luteinized follicle was detected. The interval to the subsequent ovulation was greater than 17 d for all heifers. Rhodes et al. (1995) determined that the first interovulatory interval was  $9.4 \pm 1.4$  d after refeeding nutritionally anovulatory Brahman heifers.

### ***Estrus and Luteal Function During Realimentation of Anestrus Beef Cows***

Estrus and luteal function were determined in eight nutritionally induced anestrus beef cows that were realimented with ad libitum grass hay and a protein supplement to gain approximately 1 kg/d. Mounting of cows was monitored continuously by using HeatWatch (DDx, Inc., Denver, CO) and progesterone was quantified in plasma every 3 d.

Short luteal phases (less than 10 d) were detected in seven of eight cows before the first normal luteal phase (progesterone greater than 1 ng/mL for 12 d). Only 28% of the cows exhibited estrus before the short luteal phase, and they were only mounted an average of three times. All cows had

normal luteal phases, preceded by estrus, after the short luteal phase.

Altered follicular development preceding the first ovulation in nutritionally induced anestrus cows may be associated with the absence of estrus in most cows. However, the second ovulation after anestrus is preceded by estrus and results in an estrous cycle of normal duration. The lack of estrus at first ovulation could be caused by inadequate synthesis of estradiol. When nutritionally induced anestrus heifers were realimented, plasma concentrations of estradiol at the first ovulation were less than concentrations in heifers during normal estrous cycles (Bossis et al., 2000).

### ***Role of Luteinizing Hormone***

Frequent pulses of LH are needed for maturation of preovulatory follicles (Roberson et al., 1989; Stock and Fortune, 1993). Pulsatile secretion of LH is reduced when feed intake is severely reduced in ewes (Foster and Olster, 1985) and beef cows (Day et al., 1986; Richards et al., 1989; Kurz et al., 1990). Pituitary responsiveness to GnRH is not compromised during restriction of feed intake in ewes (Haresign, 1981; Ebling et al., 1990) or beef cows (Beal et al., 1978; Whisnant et al., 1985; Rasby et al., 1992). Concentrations of GnRH in the stalk median eminence of nutritionally anestrus beef cows is greater than in fatter cows that exhibit normal estrous cycles (Rasby et al., 1992). Pulsatile infusion of GnRH every hour initiated luteal activity in nutritionally anovulatory beef cows (Bishop and Wettemann, 1993; Vizcarra et al., 1997).

Suppression of pulsatile LH secretion in cattle with a GnRH agonist resulted in a substantial decrease in the maximum size of the dominant follicle (Gong et al., 1995). Reduction in the size of dominant follicles was observed in feed-restricted postpartum beef cows compared with adequately fed cows, and this was associated with reduced LH pulse frequency (Perry et al., 1991). The relatively large increase in the size of dominant follicles in the month preceding puberty (Bergfeld et al., 1994) in beef heifers was attributed to increased LH pulse frequency (for review, see Kinder et al., 1995).

Concentrations of LH in serum of maintenance-fed and nutritionally restricted heifers were similar during the last ovulatory cycle preceding anovulation (Figure 1; Bossis et al., 1999). However, concentrations of LH were 30 and 49% less, respectively, on d 2 and 15 (proestrus; 2 d after PGF) of the cycle preceding anovulation (cycle -1) in restricted-fed heifers than in maintenance-fed heifers. Maintenance-fed heifers also had more pulses of LH than restricted-fed heifers during proestrus, but not on d 2 of the last two cycles before anovulation. When Brahman heifers were sampled on d 6 of the estrous cycle during feeding of a restricted diet and after the onset of nutritionally induced anestrus, pulsatile secretion of LH was similar to that for heifers fed maintenance diets (Rhodes et al., 1995). Day of sampling could influence the response observed.

Adequate pituitary responsiveness to GnRH during restriction of feed intake, greater concentrations of GnRH in

the stalk median eminence of anestrus than of cyclic cows, decreased concentrations of LH in serum of energy-restricted cows during maturation of the ovulatory follicle, and the ability of pulsatile GnRH to induce luteal function in anovulatory cows indicate that reduced secretion of GnRH results in inadequate pulsatile secretion of LH at the initiation of nutritionally induced anestrus.

### ***Role of Follicle-Stimulating Hormone***

Few studies have evaluated the effect of nutritional restriction on FSH secretion in cattle. Nutritionally restricted heifers had fewer pulses of LH during proestrus than maintenance-fed heifers (Bossis et al., 1999), indicating a decrease in frequency of GnRH pulses. Less-frequent pulses of GnRH are associated with increased secretion of FSH in cows (Vizcarra et al., 1999).

Secretion of FSH was similar in maintenance-fed and energy-restricted heifers during the last ovulatory cycle and on d 2 of the anovulatory cycle (Bossis et al., 1999). However, secretion of FSH was increased 2 d before anovulation in nutritionally restricted heifers compared with heifers on maintenance diets. Increased secretion of FSH preceding anovulation (during 2 d after PGF<sub>2α</sub>) could be the result of decreased pulsatile secretion of GnRH or reduced secretion of estradiol or other factors by the dominant follicle. Rhodes et al. (1996) observed increased concentrations of FSH in nutritionally induced anovulatory heifers compared with maintenance heifers. Stagg et al. (1995a) found similar secretions of FSH during normal estrous cycles and nutritionally induced anovulation in heifers. Postpartum anestrus beef cows have adequate FSH for development of dominant follicles (Stagg et al., 1995b).

Similar secretion of FSH in restricted-fed and maintenance-fed heifers before the onset of nutritionally induced anovulation and increased concentrations of FSH in serum after the onset of anovulation indicate that secretion of FSH is not rate-limiting in nutritionally restricted cattle.

### ***Metabolic Regulation of Follicular Growth***

Nutrient intake and energy stores influence concentrations of energy substrates and metabolic hormones in blood, which may alter the hypothalamic-pituitary-ovarian axis. Chronic and acute alterations in substrates and metabolic hormones may signal the brain, pituitary, and/or ovary as to the metabolic status of the animal (Figure 2). It is established that decreased pulsatile secretion of LH is associated with nutritionally induced anestrus in cows; however, the metabolic signal between body energy reserves and secretion of GnRH and LH has not been determined. In addition, metabolic signals may have direct effects on the ovary to modulate follicular growth.

Availability of amino acids that are precursors for neurotransmitters may be involved in regulating secretion of LH. Tyrosine treatment caused the frequency of LH pulses to increase in growth-restricted lambs (Hall et al., 1992). However, feeding rumen-protected L-tyrosine did not alter LH

secretion in suckled, postpartum, anestrous beef cows (Stevenson et al., 1997). The effect of tyrosine on LH secretion could be influenced by nutrient status and amount of tyrosine fed.

Chronic restriction of energy to castrated male sheep increased mRNA for neuropeptide Y (NPY) in the hypothalamus (Adam et al., 1997). Infusion of NPY into the cerebroventricle increased feed intake in sheep (Miner et al., 1989), and infusion of NPY into the third ventricle of cattle decreased pulsatile secretion of LH (Gazal et al., 1998; Thomas et al., 1999). Neuropeptide Y may influence secretion of LH in nutritionally restricted animals by altering secretion of GnRH.

Leptin, the (*ob*) gene product in mice (Zhang et al., 1994), is a possible signal between feed intake and secretion of LH. The concentration of leptin receptors in the hypothalamus was greater in feed-restricted than in well-fed ewes (Dyer et al., 1997). Additional studies are needed to determine whether leptin is a metabolic signal that controls secretion of GnRH in cattle.

Consumption of a meal by cattle has a minimal effect on concentrations of glucose in plasma. Long-term dietary treatments can have a minimal effect on plasma glucose in cattle (Yelich et al., 1996; Vizcarra et al., 1998). Although plasma concentration of glucose was extremely constant compared with that in nonruminant animals, insulin regulates utilization of glucose by cells in cattle. In addition to the role of insulin in carbohydrate metabolism, it also may influence reproductive tissues. Insulin may act in the brain to stimulate release of GnRH (Arias et al., 1992). However, intracerebroventricular infusion of insulin did not alter secretion of LH in growth-restricted ewes (Hileman et al., 1993). Insulin can act directly on the bovine ovary to stimulate proliferation and steroidogenesis of thecal and granulosa cells (Spicer and Echternkamp, 1995; Spicer and Chamberlain, 1998). Alone, insulin or LH has little effect on androstenedione production, but when treated concomitantly both dramatically increase androstenedione production (Stewart et al., 1995). Feeding heifers a restricted diet resulted in reduced concentrations of glucose and insulin in plasma during the two estrous cycles before the onset of anovulation (Bossis et al., 1999). Treatment of gilts with insulin increased ovulation rate (Cox et al., 1987) and enhanced follicular steroidogenesis (Whitley et al., 1998).

During realimentation of nutritionally induced anovulatory heifers, concentrations of glucose and insulin increased and were similar to those in cyclic heifer on maintenance diets during the two follicular waves before the wave that resulted in ovulation. Glucose and insulin are probably not major signals controlling follicular growth and ovulation, because glucose and insulin are decreased significantly in nutritionally restricted heifers for at least two estrous cycles before the onset of anestrus. In addition, concentrations of glucose and insulin in plasma of anestrous heifers during realimentation are similar to those in maintenance heifers during at least two follicular waves before the ovulatory wave.

Consumption of insufficient energy results in lipolysis and increased concentrations of NEFA in plasma. During periods of less than adequate feed intake, changes in body weight and BCS are correlated negatively with concentrations of NEFA in plasma of cows (Vizcarra et al., 1998). Feeding heifers a restricted diet resulted in increased concentrations of NEFA in plasma during the two cycles before the onset of anestrus (Bossis et al., 1999). During realimentation of nutritionally anovulatory beef heifers, body fat stores increased before the first ovulation and concentrations of NEFA in plasma were less in the previously restricted heifers that were fed to gain weight than in heifers on a maintenance diet. During the three follicular waves preceding the first ovulation, concentrations of NEFA increased gradually. Feed restriction reduced the metabolic rate in heifers (Yambayamba et al., 1996), and reduced NEFA in plasma during refeeding compared with that in maintenance heifers could reflect reduced metabolism. Concentrations of NEFA in plasma of feed-restricted cows increased before concentrations of LH were affected (Richards et al., 1989), and short-term infusion of free fatty acids to ovariectomized lambs did not alter pulsatile LH release (Estienne et al., 1990). Therefore, it is unlikely that NEFA directly affected the hypothalamic-pituitary axis to regulate secretion of gonadotropins.

Growth hormone and IGF-I have many metabolic effects associated with carbohydrate, fat, and protein metabolism. Anabolic actions of GH may be mediated through synthesis and secretion of IGF-I. Restriction of nutrient intake increases concentration of GH in cows (Armstrong and Benoit, 1996), and concentration and pulse amplitude, but not pulse frequency, of GH in serum were increased during the last two estrous cycles before the onset of nutritionally induced anovulation in heifers (Bossis et al., 1999). Feed restriction does not alter hypophyseal portal concentrations of GHRH in sheep; however, concentrations of somatotropin-release inhibiting factor are reduced compared with those in control animals (Thomas et al., 1994).

In contrast to the effect of nutritional restriction on GH, concentrations of IGF-I in blood of cattle are decreased during feed restriction (Richards et al., 1991, 1995; Armstrong et al., 1993). Restriction of protein and(or) energy intake reduces the increase in blood IGF-I that usually occurs in response to treatment with GH (Breier et al., 1988; Ronge and Blum 1989; Armstrong et al., 1993). The reduction in IGF-I in serum during nutrient restriction is associated with reduced binding of GH to hepatic membranes in steers (Breier et al., 1988). The role of IGF-I as a metabolic signal by which nutritional intake or body energy reserves control ovarian function could be through control of LH secretion or by a direct effect on the ovary. Follicles synthesize IGF-I, and systemic IGF-I could also influence ovarian function (for review see Spicer and Echternkamp, 1995). Specifically, cell proliferation and steroidogenesis are stimulated by IGF-I (Spicer et al., 1993; Spicer and Chamberlain, 1998). Although concentrations of IGF-I and its receptor in dominant follicles and subordinate follicles are similar, dominant follicles have less IGF binding protein (IGFBP) activity than subordinate follicles (Stewart et al., 1996). The decrease in

intrafollicular concentrations of IGFBP during terminal development of follicles (de la Sota et al., 1996; Funston et al., 1996; Stewart et al., 1996) may increase availability of IGF-I to follicular cells.

In extracellular fluids, IGF-I is bound to high-affinity IGFBP. Feed-restricted cattle had increased concentrations of IGFBP-2 (Vandehaar et al., 1995), and concentrations of IGFBP-2 in plasma of beef cows at 2 wk postpartum were lower and of IGFBP-3 were greater in cows that resumed estrus by 20 wk postpartum compared with anestrus cows (Roberts et al., 1997). These IGFBP inhibit the steroidogenic response of bovine granulosa (Spicer and Chamberlain, 1999) and thecal (Spicer et al., 1997) cells to IGF-I.

Nutritionally restricted heifers had reduced concentrations of IGF-I in serum during the last two cycles before anovulation compared with maintenance heifers (Bossis et al., 1999). Concentrations of IGF-I in restricted heifers during the second cycle before anovulation were significantly greater than in the anovulatory cycle. During realimentation of nutritionally induced anovulatory heifers, concentrations of IGF-I were greater in serum of maintenance-fed heifers than in restricted-fed heifers (Bossis et al., 2000). In addition, concentrations of IGF-I in serum were greater during the follicular wave when the first ovulation occurred than during the two follicular waves before ovulation (Figure 3).

Concentrations of glucose, insulin, and GH in plasma of nutritionally restricted heifers were altered before the onset of anovulation; however, concentrations were not different during the anovulatory cycle compared with the previous ovulatory cycle. Concentrations of IGF-I were less and of NEFA were greater in plasma of restricted-fed heifers than in that of maintenance-fed heifers during the two cycles before anovulation, and concentrations of IGF-I were less during the anovulatory cycle than during the previous cycle. Similarly, concentrations of NEFA were less in restricted-fed heifers during the anovulatory cycle than during the previous ovulatory cycle.

During realimentation of nutritionally induced anovulatory heifers, plasma concentrations of IGF-I and NEFA gradually increased to normal concentrations during the follicular waves before the first ovulation (Bossis et al., 2000). Concentrations of insulin and glucose in plasma of restricted heifers during realimentation were similar to concentrations in maintenance-fed heifers during the three follicular waves preceding ovulation. Temporal changes in serum IGF-I concentrations are associated with nutritional regulation of ovulatory activity in cattle. Concentrations of NEFA in plasma probably reflect body stores of fat and their rate of metabolism and may not be a metabolic signal for secretion of LH. Concentrations of NEFA in plasma are maximal during anestrus, decrease dramatically during refeeding, and then gradually increase before resumption of ovulation. Although plasma concentrations of glucose, insulin, and GH are regulated by feed intake, responses to dietary changes occur several weeks before diet influences ovarian function. Thus, NEFA, glucose, insulin, and GH are less likely than IGF-I to be major metabolic signals regulating ovarian function.

## Conclusion

Nutrient intake and body energy reserves are major regulators of ovarian function in beef cows. Long-term restriction of energy intake results in loss of body energy reserves, and pulsatile secretion of GnRH and LH are reduced. Metabolic cues (substrates, metabolic hormones, or products of metabolism) are monitored by the brain and(or) hypothalamus to influence secretion of LH. Reduced pulsatile secretion of LH prevents maturation of the dominant follicle and insufficient estradiol to cause an ovulatory surge of LH. Nutritional restriction of heifers results in decreased plasma concentrations of IGF-I, glucose, and insulin and increased concentrations of GH and NEFA during the last two cycles before anovulation compared with maintenance-fed heifers, but only concentrations of LH, IGF-I, and NEFA differed between the anovulatory cycle and the preceding cycle. In addition, realimentation resulted in altered concentrations of IGF-I, NEFA, glucose, and insulin in plasma, but only concentrations of IGF-I and NEFA increased gradually during successive follicular waves until the dominant follicle ovulated. We propose that IGF-I may be one of many signals that influence pulsatile secretion of GnRH and LH, controlling follicular growth in cattle. The major effect of nutrition on ovarian function is via alteration of LH secretion; however, nutrition may have modulating effects on the ovary through metabolic signals such as IGF-I. Continued research to provide a better understanding of metabolic regulation of ovarian function is essential to develop management systems and techniques to enhance reproductive performance.

## Implications

Chronically underfed heifers and cows continue estrous cycles until they lose sufficient body energy reserves and become anovulatory. Restricted nutrient intake alters follicular development before anestrus occurs and could influence reproductive performance. Less body fat stores are required to maintain ovarian cycles than to reinitiate cycles after nutritionally induced anovulation. Greater daily gain during realimentation of nutritionally induced anovulatory cattle results in a shorter interval to resumption of ovulation.

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### Notes

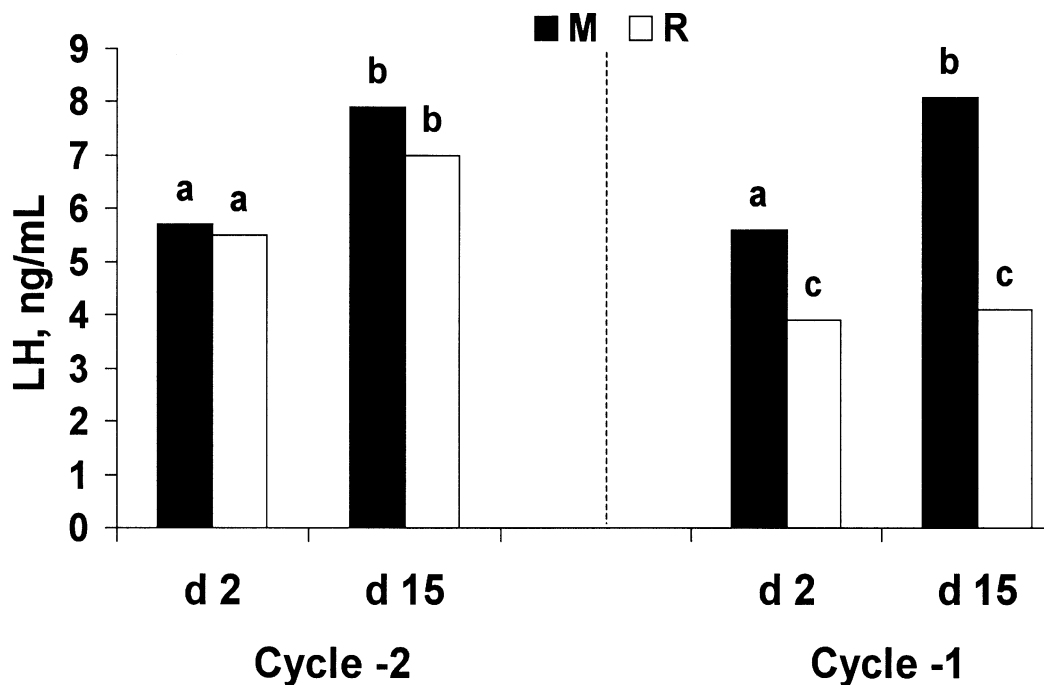
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**Table 1.** Characteristics of dominant follicles during follicular waves in nutritionally restricted anovulatory beef heifers before realimentation (Wan), two waves (W-2), or one wave (W-1) before ovulation, and the ovulatory wave (W0)<sup>a</sup>

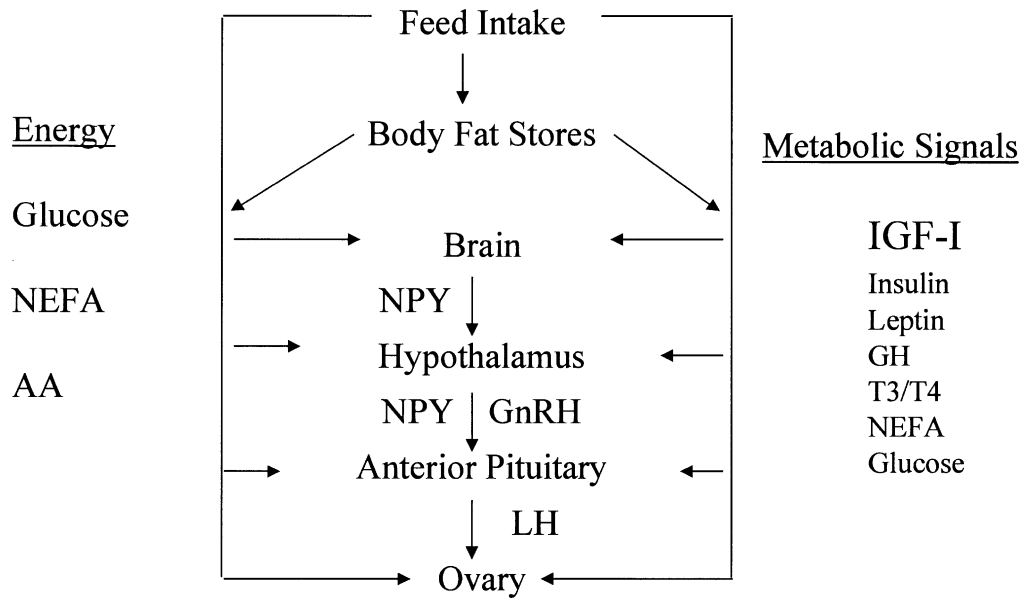
Criterion	Wave				MSE
	Wan	W-2	W-1	W0	
Growth rate, mm/d	9 <sup>b</sup>	1.2 <sup>c</sup>	1.5 <sup>d</sup>	1.6 <sup>d</sup>	.04
Duration of growing phase, d	5.2 <sup>b</sup>	6.4 <sup>c</sup>	6.4 <sup>c</sup>	7.0 <sup>c</sup>	.7
Maximum diameter, mm	9.2 <sup>b</sup>	11.7 <sup>c</sup>	13.2 <sup>d</sup>	15.3 <sup>e</sup>	1.1
Regression rate, mm/d	1.0 <sup>b</sup>	1.2 <sup>c</sup>	1.5 <sup>d</sup>	—	.02
Wave persistence, d	14.0 <sup>b</sup>	17.2 <sup>c</sup>	17.4 <sup>c</sup>	—	4.8

<sup>a</sup>Adapted from Bossis et al. (2000).

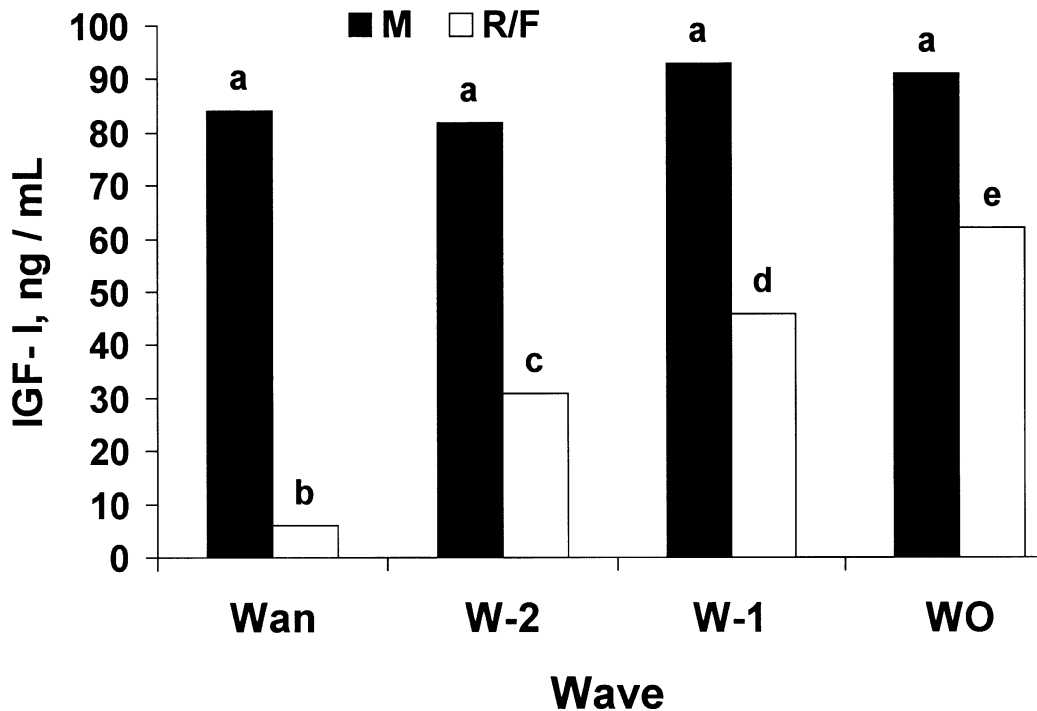
<sup>b,c,d,e</sup>Means within a row lacking a common superscript ( $P < .05$ ).



**Figure 1.** Concentrations of LH in serum of maintenance (M) and nutritionally restricted (R) heifers during the last two estrous cycles before the onset of anovulation. Heifers were treated with PGF<sub>2α</sub> on d 13 (d 0 = estrus). Concentration of LH were quantified in samples obtained at 10-min intervals for 8 h on d 2 and d 15 (proestrus). Cycle -2 was the last ovulatory cycle in R heifers, and cycle -1 ended when the second-wave dominant follicle did not ovulate. Bars without common superscripts differ ( $P < .05$ ). Adapted from Bossis et al. (1999).



**Figure 2.** Feed intake and body energy stores influence the availability of energy to the brain, pituitary and ovary, as well as metabolic signals that can influence these tissues. Alterations in energy available to tissues and(or) concentrations of metabolic signals regulate ovarian function in beef cattle. (NPY = neuropeptide Y, T3 = triiodothyronine, T4 = thyroxine).



**Figure 3.** Concentrations of IGF-I in plasma of beef heifers during estrous cycles (M), in nutritionally restricted heifers (R/F) during anovulation (Wan), and during realimentation at two (W-2) or one (W-1) follicular waves before the ovulatory wave (W0). Adapted from Bossis et al. (2000).