Effects of early weaning on finishing feed efficiency, marbling development and retail product quality of beef steers

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ABSTRACT

Beef cattle producers continuously search for nutritional management options that provide flexibility to production scenarios. Due to its positive effects on maternal productivity, early weaning is one such alternative strategy that has received considerable interest. To better understand the effects of early weaning on calf productivity, an extensive literature review and three experiments were conducted to evaluate the effects of early weaning on finishing feed efficiency, marbling development and retail product quality of beef steers. In experiment I, which included 90 Angus-sired steers from four calving seasons, early weaning followed by a short *ad libitum* concentrate-feeding and pasture-backgrounding phase reduced finishing residual feed intake (RFI) by 7 % (*P* < 0.0001) and increased carcass marbling score (MS) by 10 % (*P* < 0.01) when compared to conventionally weaned (CW) contemporaries. Similar effects were observed in experiment II, which included 28 Angus and Simmental-sired steers, as early weaning reduced RFI (*P* < 0.01) and increased carcass MS (*P* < 0.01). Lung mass of early weaned (EW) steers was greater than their CW contemporaries (*P* < 0.05), and was inversely related to RFI (*R^2* = 0.17; *P* < 0.05). Finishing treatments in this experiment included a high corn ration and an alternative low corn ration that iso-calorically replaced 50 % of the DM from corn with dried corn gluten feed. Iso-caloric replacement of corn reduced lung mass (*P* < 0.01), and when combined with the observed increase of EW steers suggests that lung development is
affected by dietary energy type at various stages of growth. In experiment III, objective analyses of ribeye steaks obtained from steers included in experiment two revealed that early weaning increased cross-sectional muscle fiber area by 28 % \( (P < 0.001) \) and tended to increase \( (P = 0.08) \) Warner-Bratzler shear force by 36 %. Nonetheless, these effects were not great enough to alter un-trained consumer perception of texture \( (P \geq 0.65) \), juiciness \( (P \geq 0.55) \), flavor \( (P \geq 0.25) \) or overall acceptability \( (P \geq 0.34) \). Collectively, these results indicate that early weaning enhances finishing feed efficiency and carcass marbling without affecting un-trained consumer sensory perception.
DEDICATION

This dissertation and the efforts reported herein are dedicated in honor of Second Lieutenant Ethan C. Smith, United States Marine Corps, his service, and the leadership he provided to Marines of the Second Marine Expeditionary Force, R4OG, Operation Enduring Freedom XIII, Helmand Province, Afghanistan.
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CHAPTER I: LITERATURE REVIEW

Introduction

Unlike many other sectors of animal agriculture, management strategies incorporated in beef production systems vary widely throughout much of the U.S. due primarily to variation in climate and feed resource availability. As such, beef producers are continually searching for alternative nutritional management strategies that are capable of enhancing animal well-being, production efficiency, profitability, and beef product quality. Researchers and producers alike have historically expressed interest in early weaning as an alternative early nutritional management option for beef cattle. As a result, a number of researchers have devoted efforts toward better understanding the effects of early weaning on the cow and the calf throughout the last half of a century. In order to explore and condense relevant findings of this research, results of these efforts are summarized in the following review.

Effects of early weaning on maternal productivity

Early weaning, or permanent removal of a calf from its dam at less than the conventional age of 205 d, is often utilized as a reproductive management strategy, particularly by cow/calf producers that exist in a subtropical environment (Arthington, 2012). The adoption of this practice by beef cow/calf producers in certain parts of the United States was the result of numerous research efforts that reported increases in overall conception rate (Smith and Vincent, 1972; Laster et al., 1973; Lusby et al., 1981) and the percentage of cows exhibiting estrus (Laster et al., 1973), as well as a decrease in the postpartum interval to conception (Smith and Vincent, 1972) when calves were weaned prior to the initiation of a natural-service or AI breeding season.
Such improvements in reproductive performance are independent of effects on the number of services per conception, and as such are the result of not only an increased occurrence of estrus during the breeding season (Laster et al., 1973), but also a decreased postpartum interval to the return of estrus cyclicity (Martins et al., 2012).

These effects, however, are age dependent, as the greatest improvements are observed for 2-yr-old primiparous and 3-yr-old multiparous cows (Laster et al., 1973), potentially due to the fact that beef females at this age are still considered immature. Various other authors have reported elevations in ADG (Peterson et al., 1987; Myers et al., 1999a; Llewellyn et al., 2013), body condition score (BCS) at the time of conventional weaning (Story et al., 2000; Arthington et al., 2003; Martins et al., 2012), change in BCS between the times of early and conventional weaning (Myers et al., 1999a; Myers et al., 1999c; Schultz et al., 2005; Llewellyn et al., 2013) and pregnancy rate, as well as a decrease in calving interval (Arthington et al., 2003) for dams of calves that were early weaned (EW) prior to the initiation of the breeding season when compared to dams of calves that were conventionally weaned (CW) upon its conclusion. When combined with the observation that the magnitude of these effects diminishes with increasing parity, the increase in ADG and change in BCS of dams of EW calves suggests that these improvements in reproductive performance can be attributed to reduced nutrient demand on the dam following the cessation of lactation, as the nutrient demands of lactation represent a substantial portion of the overall energy requirements of the female. This is further supported by the observation that BCS is a reflection of energy status and reproductive performance (Randel, 1990), and evidence that elevations in BCS positively influence the frequency of luteinizing hormone (LH) pulses, ovarian activity, and ultimately the return to estrus cyclicity for anestrous cows (Bishop et al., 1994).
Aside from the effects of early weaning that have been observed for the dam, researchers and producers alike have expressed interest in better understanding the effects of early weaning on the subsequent maternal productivity of calves retained as replacement females. Early weaned heifer calves managed on a high post-weaning plane of nutrition attain puberty at a younger age than their CW contemporaries (Sexten et al., 2005; Gasser et al., 2006c; Moriel et al., 2014b). Although creep-feeding replacement heifers reduces first-parity milk production (Sexten et al., 2004), early weaning has no adverse effect on first- or second-parity milk production or progeny performance (Sexten et al., 2005). Furthermore, EW heifer calves fed a high-concentrate ration undergo a lesser degree of estradiol-driven negative feedback on the secretion of LH (Gasser et al., 2006a), resulting in a greater frequency of LH pulses (Gasser et al., 2006c) and a larger diameter dominant follicle than CW contemporaries (Gasser et al., 2006b) preceding the attainment of puberty. Conventionally weaned heifers consuming high-energy rations attain puberty at a younger age than CW heifers consuming low-energy rations (Wiltbank et al., 1966; Laster et al., 1972), supporting the theory that a high plane of nutrition accelerates puberty.

An inverse relationship exists between rate of growth and the age at puberty for replacement heifer calves (Arije and Wiltbank, 1971; Buskirk et al., 1995). Secretion of insulin-like growth factor I (IGF-I) in growing cattle increases as a result of increased dietary energy density (Houseknecht et al., 1988), and is associated with increased levels of growth (Breier et al., 1986). Moriel et al. (2014b) reported that plasma IGF-I concentrations explained 34% of the variation in age at puberty for a combination of CW and EW heifers under various post-weaning nutritional management strategies. Rhodes et al. (1978) provided evidence that rate of growth and body weight (BW) are not solely responsible for age at puberty. In this experiment, heifers
that received a rumen-protected fat supplement but experienced a similar ADG to unsupplemented contemporaries demonstrated more than a 45 % reduction in the number of animals reaching puberty during a 168-d test period. Supplementation of monensin, a polyether antibiotic fermentation product of *Streptomyces cinnamonomensa* commonly utilized in beef nutritional management programs, consistently shifts rumen fermentation patterns to favor propionate production and decrease the molar proportion of acetate to propionate (Dinius et al., 1976; Raun et al., 1976; Richardson et al., 1976; Moseley et al., 1982). Monensin supplementation decreases the age at attainment of puberty for replacement heifers developed on a roughage-based diet (Moseley et al., 1977; Moseley et al., 1982), independently of elevations in BW or ADG. McCartor et al. (1979) reported that feeding beef heifers diets that consisted of 80 % roughage and 20 % concentrate with monensin or feeding a diet that consisted of 50 % roughage and 50 % concentrate without monensin resulted in 24- and 35-d reductions in the age at attainment of puberty, respectively, which did not differ from one another, when compared to feeding a diet that consisted of 80 % roughage, 20 % concentrate without monensin. Due to the effects of dietary energy density on the secretion of IGF-I and ruminal production of propionate, as well as propionate’s stimulative effect on insulin (Lee and Hossner, 2002), it is more likely that the occurrence of precocious puberty (< 300 d of age) associated with early weaning is a function of increased actions of insulin and IGF-I on ovarian function (Gong et al., 1993; Spicer and Echternkamp, 1995; Webb et al., 1999; Gong et al., 2002).

Collectively, this information suggests that early weaning prior to the initiation of the breeding season may be a viable management option that could be utilized to increase the reproductive performance of beef females, and will likely be most effective when applied to females undergoing a nutritional insult, or during times of feed resource inadequacy.
Furthermore, early weaning can also be utilized as an effective reproductive management strategy to decrease the age at attainment of puberty for replacement heifers, which is likely the result of a combination of an enhanced nutritional status and elevated ruminal production of propionate. Based upon this information, the greatest opportunity for the strategic utilization of early weaning as a reproductive management strategy exists in scenarios where conception is an issue in first- and second-parity females, during times of limited forage resources to support the cow herd, or to decrease the calving interval of existing herds.

**Effects of early weaning on calf growth**

Green and Buric (1953) suggested that environmental influences early in the life of a calf could be evident for a reasonably long period of time post-weaning. These authors compared the growth potential and ADG of steer and heifer calves EW at 90 d of age to previously unsupplemented contemporaries that were CW at 180 d of age in an effort to not only test this hypothesis, but also to evaluate the ability of early growth evaluations to decrease the age at which useful knowledge could be acquired to estimate the breeding value and genetic merit of beef cattle. All calves were provided *ad libitum* access to a concentrate-based growing ration and chopped alfalfa hay beginning at weaning and ending at 370 d of age. Although the authors reported elevations in BW and ADG, as well as the consistency of post-weaning growth for EW calves, no differences were observed in BW at 370 d of age, and it was concluded that early weaning was not, at that time, suggested as a practical, routine method for raising beef calves.

Following this initial report, various other authors reported elevations in ADG for EW calves that received *ad libitum* access to a concentrate supplement on pasture when compared to contemporaries that remained unsupplemented with dams on pasture until the time of
conventional weaning (Harvey et al., 1975; Neville and McCormick, 1981). Additionally, other authors have reported similar effects for EW calves when CW calves were limit-fed concentrate (Peterson et al., 1987) or supplemented with concentrate *ad libitum* on pasture until conventional weaning (Williams et al., 1975). In contrast, Harvey and Burns (1988) reported no ADG advantage of EW calves when CW calves were allowed to creep-graze native pasture, *Trifolium pretense* (red clover) and *Poa pratensis* (Kentucky bluegrass), or *Pennisetum Americanum* (Tifleaf pearl millet) pastures during the EW feeding period. However, the lack of an effect of early weaning on ADG in this scenario was likely a function of a relatively low plane of nutrition, as EW calves were supplemented with ground ear corn at a rate of only 1 % of BW per d and allowed to graze Tifleaf pearl millet pasture. Nonetheless, these authors reported a 39.1 kg per ha advantage in overall post-weaning calf gain for EW calves when stocked at a similar density to their CW contemporaries that remained with their dams.

Although the majority of the aforementioned experiments involved supplementing EW calves with concentrate on pasture, various other authors have reported increased ADG of EW steers that were fed concentrate *ad libitum* in a dry-lot setting when compared to CW calves that remained unsupplemented prior to weaning (Grimes and Turner, 1991; Myers et al., 1999c; Story et al., 2000; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Llewellyn et al., 2013; Scheffler et al., 2014; Nayananjalie et al., 2015a; Nayananjalie et al., 2015b). Moriel et al. (2014a) reported an advantage in ADG of EW steers that were fed concentrate at a rate of 3.5 % of BW per d in a dry lot for 180 d when compared to CW steers that remained unsupplemented with their dams for an experiment that was replicated over two years. Although, no improvement in ADG over the same 180-d period was noted for EW steers that were limit-fed concentrate for 90 d and allowed to graze *Paspalum notatum* (Bahiagrass)
pasture for the remaining 90 d, these authors observed a reduction in ADG of EW steers that were allowed to graze only Bahiagrass pasture in year 1 and *Lolium multiflorum* (Annual ryegrass) followed by Bahiagrass in year 2 without concentrate supplementation throughout the duration of the EW feeding period. Additionally, Myers et al. (1999a) reported a similar effect when the mean of EW steers was contrasted against that of unsupplemented and creep-fed CW steers, while Shike et al. (2007) reported no effect of early weaning on ADG when contrasted against a combination of steers that were creep-fed with either a concentrate- or fiber-based supplement, indicating that EW steers must be managed on a high plane of nutrition in order to observe an improvement in ADG.

Harvey et al. (1975) provided similar evidence to that of Green and Buric (1953), where CW contemporaries later compensated for the limited rate of growth experienced between the times of early and conventional weaning. The presence of post-weaning compensatory growth of CW calves was observed during the finishing phase by various other researchers that finished cattle immediately following weaning (Story et al., 2000; Barker-Neef et al., 2001; Schoonmaker et al., 2001), or included an additional growth or backgrounding phase between the time of conventional weaning and finishing (Schoonmaker et al., 2004; Scheffler et al., 2014; Nayananjalie et al., 2015a; Nayananjalie et al., 2015b). Although one author noted a reduction in overall ADG of EW steers (Myers et al., 1999c), others reported no effect (Scheffler et al., 2014) or a 7 to 10 % advantage in overall ADG (Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004) over CW calves between the time of early weaning and harvest when EW calves were provided concentrate *ad libitum* post weaning.

Myers et al. (1999c) and Schoonmaker et al. (2001) reported no effects of early weaning on overall hip height change between the time of early weaning and harvest, while Schoonmaker
et al. (2004) reported a shorter (< 2 %) final hip height of EW steers at the time of harvest. These authors, however, did not report hip height measured at other times throughout the experiment, suggesting that this effect could have been the result of differences in hip height that existed prior to initiation of the treatments. Regardless, the minimal magnitude of this effect, if it does indeed exist, lacks meaningful biological and economic significance. The absence of a biologically significant effect of early weaning on skeletal growth indicates that the increase in ADG is the result of an increase in the growth and/or proportionality of lean muscle, adipose, visceral organs, or some combination thereof.

When compared to CW steers, Schoonmaker et al. (2004) and Meyer et al. (2005) reported elevations in ultrasound-estimated LMA (unadjusted) and 12th-rib subcutaneous fat thickness (SFT) at the time of conventional weaning for steers that were EW and fed concentrate *ad libitum* until the time of conventional weaning. Nayananjalie et al. (2015a) reported an increase in the phosphorylation ratios of two signaling proteins involved in muscle hypertrophy, ribosomal protein S6 and S6 kinase 1, for EW steers during the early post-weaning dry-lot feeding period, which independently explained 25 and 22 % of the variation in ADG, respectively. Ribosomal protein S6 and ribosomal protein S6 kinase 1, two key components of the *mammalian target of rapamycin* (*mTOR*) signal transduction pathway involved in muscle protein synthesis (Bolster et al., 2002) are activated in response to insulin and/or amino acids such as leucine (Bolster et al., 2004).

Based upon these concepts, it is plausible to speculate that a portion of the improvement in ADG often observed for EW calves can be attributed to both lean muscle tissue and adipose accretion. Furthermore, the lack of carryover effects on the phosphorylation ratios of ribosomal protein S6 and S6 kinase 1 following completion of the early dry-lot feeding period for EW
steers reported by Nayananjalie et al. (2015a) suggests that the increased phosphorylation of these signaling proteins during the early dry-lot feeding period could be the result of increased insulin secretion in response to an elevated plane of nutrition between the times of early and conventional weaning. However no reports that compared insulin or metabolite concentrations at similar time points could be found.

Nonetheless, when combined with the numerous observations of post-weaning compensatory growth for CW steers and the elevation in ultrasound-estimated LMA for EW steers at the time of conventional weaning reported by Schoonmaker et al. (2004) and Meyer et al. (2005), it is likely that a substantial portion of the often observed advantage in overall ADG of EW steers is the result of enhanced muscle hypertrophy during the EW feeding period. Moreover, these results provide collective evidence that although CW calves undergo compensatory growth post weaning, early weaning is capable of yielding up to a 10 % advantage in overall ADG without a corresponding and meaningful increase in skeletal growth and frame size.

**Effects of early weaning on body composition and carcass traits**

Few researchers have compared body composition of EW to CW cattle prior to harvest. Of the limited investigations that exist, researchers have reported elevations in ultrasound-estimated SFT and LMA (Schoonmaker et al., 2004; Meyer et al., 2005), but not percent IMF (Schoonmaker et al., 2004) at the time of conventional weaning for EW calves that were supplemented with concentrate *ad libitum* in a dry lot. Although not measured by these authors, the increase in LMA observed for EW steers at the time of conventional weaning was likely a function of increased phosphorylation of signaling proteins involved in muscle hypertrophy.
(Nayananjalie et al., 2015a) in response to the enhanced nutritional status of EW calves during the dry-lot feeding period. To further reiterate the importance of research in this area, no reports could be found that compared ultrasound-estimated SFT, LMA or IMF of EW to CW cattle at the completion of each production phase for experiments that included a backgrounding phase prior to finishing.

In contrast to the limited reports that exist for pre-harvest body composition of EW cattle, numerous researchers have evaluated the effects of early weaning on finished beef carcass traits. Schoonmaker et al. (2004) reported a smaller LMA of carcasses from EW than CW steers, however these results conflict with the reports of others who observed no effect of early weaning on carcass LMA or ribeye area [REA (Harvey et al., 1975; Lusby et al., 1990; Loy et al., 1999; Myers et al., 1999a; Myers et al., 1999b; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Arthington et al., 2005; Meyer et al., 2005; Waterman et al., 2012)]. Furthermore, the outlying results reported by Schoonmaker et al. (2004) were likely the result of EW steers being harvested at a lighter finished weight than their CW contemporaries, as REA is positively correlated with live BW (Orme et al., 1959).

Reports of both a tendency toward a reduction in KPH (Harvey et al., 1975), as well as an elevation in KPH (Myers et al., 1999a) and YG (Myers et al., 1999a; Story et al., 2000) exist for carcasses of EW cattle. It is important to note, however, that the low magnitude of the reported differences have little to no biological or economic significance. Others observed no differences in KPH and YG between carcasses of EW and CW cattle when CW cattle remained unsupplemented prior to finishing (Lusby et al., 1990; Loy et al., 1999; Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Waterman et al., 2012).
In contrast to other carcass traits, marbling score (MS) increased from 4 to 10 % for EW cattle when both EW and CW cattle were finished immediately following weaning (Loy et al., 1999; Myers et al., 1999a; Meyer et al., 2005; Shike et al., 2007). Scheffler et al. (2014) reported a 20 % improvement in carcass MS that corresponded with a 25 % increase in chemically-extracted IMF for EW steers that were fed concentrate *ad libitum* in a dry lot for 148 d before being backgrounded on pasture for an additional 156 d and finished to a common SFT.

Other researchers have reported no effect of early weaning on carcass MS (Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Arthington et al., 2005; Moriel et al., 2014a), or a reduction in MS (Waterman et al., 2012). It is important to note, however, that this may in part be the result of finishing steers to a target SFT-based harvest endpoint immediately following the time of conventional weaning, which resulted in EW cattle being harvested at a younger age or after being finished for a shorter duration. Owens and Gardner (2000) reported that carcass MS typically increases with duration of concentrate feeding. Although Barker-Neef et al. (2001) and Schoonmaker et al. (2004) reported a lower level of IMF in ribeye steaks of EW steers that were provided concentrate *ad libitum* post weaning, Scheffler et al. (2014) reported a 25 % increase (not statistically significant) in IMF when an additional pasture growing phase was included prior to finishing. This indicates that the lack of an effect on or decrease in IMF observed by other authors may have been the result of cattle reaching a harvest endpoint at an age early enough to limit marbling development. Furthermore, decreasing the energy content of feed provided during the post-weaning growth period for EW steers prior to finishing reduces finished carcass MS (Bedwell et al., 2008; Retallick et al., 2010).
Although numerous genes are differentially expressed relative to the marbling potential of cattle (Wang et al., 2009), the ligand-activated nuclear receptor peroxisome proliferator-activated receptor γ (PPARγ) is not only necessary for adipose development (Rosen et al., 2000), but has also been referred to as the master-regulator of adipogenesis (Rosen and MacDougald, 2006). Wang et al. (2009) reported that PPARγ expression increases upon feedlot entry and the initiation of an energy-intensive finishing program for cattle that have undergone a long-term grazing period prior to finishing. Insulin is the primary activator of PPARγ mRNA expression in human adipocytes, and results in a dose-dependent increase when administered in vitro (Rieusset et al., 1999). When evaluated in cattle, Ren et al. (2002) reported substantially greater circulating plasma insulin concentrations for cattle with greater marbling potential (Holstein) when compared to cattle with lower marbling potential (Charolais), which was later confirmed by Bellmann et al. (2004). Waterman et al. (2012) reported numerically greater serum insulin concentrations for EW than CW steers after EW steers had received ad libitum access to a high-concentrate ration in a dry lot for 133-d while CW steers remained unsupplemented on pasture with their dams. Moriel et al. (2014a) reported that early weaning followed by a 180-d concentrate feeding period in a dry lot resulted in more than a 2-fold increase in LM PPARγ mRNA expression when measured upon completion of the feeding period and compared to conventional weaning. Moisá et al. (2014) reported that the expression of CCAAT/enhancer-binding protein α (CEBPα), a known regulator of adipogenesis, and PPARγ, along with a number of additional downstream adipogenic and lipogenic genes and enzymes increased soon after the time of weaning for EW steers managed under a similar strategy, but not CW steers.

Upregulation of the PPARγ regulatory network in response to increased insulin resulting from an enhanced nutritional status would likely stimulate IMF deposition without affecting
subcutaneous adipogenesis, as these adipose depots differ widely in insulin sensitivity (Rhoades et al., 2007). Although Moriel et al. (2014a) reported no difference in carcass MS between EW and CW steers, the lack of an effect could have been associated with biological type, as cattle included in the experiment were progeny of at least one parent with Bos indicus genetic influence, and therefore could be assumed to have had a lower genetic propensity for marbling, as marbling potential is thought to be inversely related to degree of Bos indicus influence (Marshall, 1994).

Scheffler et al. (2014), who included an additional pasture backgrounding phase between completion of the EW dry-lot feeding period and the finishing phase reported the greatest elevation in carcass MS of EW steers (20 %) when compared to all other existing reports. These authors went on to describe that this effect was potentially the result of metabolic imprinting events that occurred as a result of the nutritional management of EW calves, and proposed four mechanisms that could have been responsible for the enhancement in marbling development. These mechanisms included 1) creation of an increased population of preadipocytes through proliferation during the early dry-lot feeding period, which was maintained throughout the pasture backgrounding phase and formed mature adipocytes during the finishing phase (Gorocica-Buenfil et al., 2007), 2) the early dry lot feeding period may have caused increased recruitment of mesenchymal stem cells to adipocytes (Tang and Lane, 2012), 3) EW calves may have been programmed to respond with greater magnitude to signaling molecules or for enhanced digestion, absorption, or metabolism to accumulate lipid (Long et al., 2012a; Volpato et al., 2012), or 4) that IMF development may be merely dependent upon the total amount of energy consumed by an animal, and independent of stage of growth or production.
Although no clear definition exists for the term metabolic imprinting (Waterland and Garza, 1999), the term is commonly used to describe postnatal nutritional events that lead to epigenetic changes that affect physiology of an individual later in life, or of future progeny. The foundation of this concept stems from the observation of the fetal and infant origins of adult disease; more commonly referred to as the “Barker hypothesis,” which emphasizes an association between the pre- or early post-natal environment and physiology or the onset of disease later in life (Barker, 1990). While the majority of efforts to better understand the implications of metabolic imprinting have been devoted toward human health, it is possible that such events may be responsible for the improvement in carcass MS of EW steers, as suggested by Scheffler et al. (2014).

In support of the theory that the improvements in carcass MS of EW steers may be the result of metabolic imprinting, rather than being merely a function of increased energy consumption, Meteer et al. (2013) reported approximately a 15% elevation in carcass MS of EW steers when compared to their creep-fed CW contemporaries. Furthermore, *in vitro* evidence suggests the ability of mature adipocytes to dedifferentiate to a preadipocyte stage during times of limited substrate abundance (Fernyhough et al., 2004; Dodson et al., 2005) and re-differentiate to form adipocytes that accumulate lipid in the presence of substrate (Fernyhough et al., 2007). Although these results have yet to be reproduced *in vivo*, it is possible that a portion of intramuscular adipocytes developed during the early concentrate feeding period of EW steers could dedifferentiate to a preadipocyte stage in response to a lower plane of nutrition throughout the pasture backgrounding phase. Upregulation of the CEBPα and PPARγ regulatory network in response to acclimation to a nutrient-dense finishing ration could then result in preadipocyte
redifferentiation, and ultimately an increased population of intramuscular adipocytes that possess the ability to accumulate lipid and be recognized as marbling.

Backgrounding and growing programs are not generally associated with improvements in marbling (Klopfenstein et al., 2000), and marbling development during the finishing phase is independent of dietary energy type during the growing phase in conventional beef production systems when cattle are finished to a common SFT-based endpoint (Wertz et al., 2001; Vasconcelos et al., 2009). It is possible, however, that their inclusion between nutritional phases that favor a positive energy balance may lead to the enhanced proliferative ability of adipocytes. Alternatively, the inclusion of post-weaning dry-lot feeding and pasture-backgrounding phases for EW calves could result in imprinted upregulation of the CEBPα and PPARγ regulatory networks, stimulating adipocyte differentiation to produce an adipocyte population that is retained throughout backgrounding. These theories, however, remain to be evaluated in vivo.

The latter of the theories proposed by Scheffler et al. (2014) would suggest that IMF development is independent of energy type, and rather dependent upon energy density. Irrespective of weaning management scheme, controversy exists within the animal and dairy science communities over the preference of cattle to utilize particular energy substrates (i.e. glucose vs. acetate) for lipogenesis. Much of the controversy questioning the ability of cattle to utilize glucose as an acetyl unit donor for fatty acid synthesis has originated from early work related to the presence and activity of certain lipogenic enzymes in the liver and mammary gland of dairy cattle and other non-ruminant species.

Hanson and Ballard (1967) reported that while active in the liver of the rat, one of the major enzymes involved in the conversion of glucose to acetyl CoA, ATP citrate lyase, is inactive in the liver of dairy cattle. Up until that time, researchers were still under the impression
that similar to monogastric animals, the majority of \textit{in vivo} lipogenesis also occurred in the liver for ruminants. Ingle et al. (1972) reported that the liver of ruminant animals plays only a small role in \textit{in vivo} lipogenesis while adipose tissue is responsible for over 90 percent of fat synthesis, leading to the realization that adipose tissue is the major site of lipogenesis in ruminants.

Furthermore, early reports of experiments conducted \textit{in vitro} suggested acetate to be the preferred energy substrate for fatty acid synthesis in bovine visceral (Hanson and Ballard, 1967) and subcutaneous adipose (Hood et al., 1972), and glucose to be the preferred substrate for triglyceride-glycerol synthesis (Hood et al., 1972). Hood et al. (1972) further described that very little glucose was used directly for fatty acid synthesis by subcutaneous adipose \textit{in vitro}, but went on to emphasize the importance of glucose and its role in adipogenesis, as it is considered to be a major source of NADPH through the pentose-shunt biochemical pathway.

Propionate is considered the major gluconeogenic energy precursor for ruminants. Some of the proceeding \textit{in vitro} cell culture work conducted by Smith and Crouse (1984) indicated that intramuscular adipocytes may have a preference for glucose as an acetyl unit donor, as glucose provided 50 to 75 \% of the acetyl units used for intramuscular adipogenesis and only 1 to 10 \% of the acetyl units used for subcutaneous adipogenesis. These authors additionally reported a preference of subcutaneous adipocytes for acetate, as acetate provided 70 to 80 \% of the acetyl units for subcutaneous adipogenesis and only 10 to 25 \% of the acetyl units for intramuscular adipogenesis. However interpretation of the results reported by Miller et al. (1991) suggests a preference for acetate over glucose as a precursor for fatty acid synthesis by both subcutaneous and intramuscular adipose. This alternative theory that supports the lack of preference of intramuscular adipocytes for glucose as an energy substrate was more recently supported by Nayananjalie et al. (2015b), who reported similar \textit{in vivo} fractional palmitate synthesis rates from
acetate and glucose in visceral, subcutaneous and intramuscular adipose, and that respective adipose depots do not differ in substrate preference between early and CW steers.

The previous reports of the preference of IMF for glucose as an energy substrate, although yet to be replicated in vivo, have resulted in the assumption that grain-based finishing programs result in beef carcasses with greater IMF and MS when compared to roughage- and byproduct-based finishing programs, predominantly due to the high level of starch. This theory dates back to the early work of Oltjen et al. (1971), and has been supported by work related to the replacement of grain with byproducts of the grain-milling industry that have been processed in such a way that results in the removal of the majority of their starch content. It is important to note, however, that roughages and many byproducts have a much lower energy content and digestibility than most cereal grains. Although there have been multiple reports that replacement of 30 to 50% of the dietary DM from corn with wet distillers grains with solubles (WDGS) has little to no effect on MS of finished cattle (Al-Suwaiegh et al., 2002; Corrigan et al., 2009), more recent results reported by Schoonmaker et al. (2010) indicated an inverse relationship between increasing WDGS inclusion (as a replacement for corn and soybean meal) and carcass MS for cattle finished with concentrate-based rations. Additionally, results reported by Luebbe et al. (2012) indicate a linear reduction in MS associated with replacement of dry-rolled corn with WDGS in finishing diets. Although useful from an applied standpoint, a major limitation of the study’s utility toward further understanding the favorability of diet type for marbling development is that the treatment that replaced almost half of the DM from corn with WDGS (highest WDGS inclusion) resulted in a 9% reduction in average daily NE\textsubscript{g} intake when compared to that of the control group. Interestingly, cattle assigned to this treatment group also displayed a 9% reduction in carcass MS when compared to cattle that received rations that
replaced no corn with WDGS, suggesting that the reduction in marbling development may have been a function of energy dilution resulting from the inclusion of a low-starch feedstuff.

Regardless of source of energy, consumption of concentrate *ad libitum* in a dry lot by EW calves while CW calves remain unsupplemented with their dams would be expected to result in an increase in overall energy intake. Due to the inherent difficulty that exists in measuring intake of suckling calves, this has yet to be confirmed experimentally. Nonetheless, managing EW cattle under a high post-weaning plane of nutrition appears to enhance marbling development when cattle are harvested at a common SFT-based endpoint. Further research is warranted to determine the role that metabolic imprinting events may play in this economically advantageous improvement.

**Effects of early weaning on beef product quality**

Marbling, or the subjectively measured visual representation of IMF, contributes to the tenderness, juiciness and flavor intensity of beef products (Blumer, 1963), but explains only a small portion of the variation in consumer acceptance (Platter et al., 2003). Although various authors have reported elevated MS of carcasses from EW steers (Loy et al., 1999; Myers et al., 1999a; Meyer et al., 2005; Shike et al., 2007; Scheffler et al., 2014), it seems plausible to speculate that the magnitude of difference in consumer acceptance that would be attributed to small differences in carcass MS would be minimal.

Independently of MS, Barker-Neef et al. (2001) reported that ribeye steaks of EW steers had lower luminance colorimetric values ($L^*$) than CW steers, while redness ($a^*$) and yellowness ($b^*$) values did not differ. Furthermore, these authors reported no effect of early weaning on Warner-bratzler shear force (WBSF), an objective measurement of tenderness (Barker-Neef et
al., 2001). Such colorimetric values are inversely correlated to WBSF and conversely correlated to trained-panel perception of tenderness (Wulf et al., 1997). Additionally, these objective colorimetric values are more highly correlated to beef tenderness than subjective measurements of marbling (Wulf et al., 1997). It is possible, however, that the low magnitude of the difference (3.5 %) in L* values of ribeye steaks from EW steers observed by Barker-Neef et al. (2001) was not great enough to result in a noticeable difference in WBSF. However Schoonmaker et al. (2004) later reported a 10 % increase in WBSF of ribeye steaks from EW steers that were provided concentrate ad libitum when compared to previously unsupplemented CW steers after being finished to a common SFT-based endpoint.

Vestergaard et al. (2000) reported that a forage-based diet promotes oxidative muscle metabolism, thus limiting glycolytic potential, which would ultimately result in changes in muscle color. Furthermore, glycolytic potential is inversely related to beef product tenderness (Wulf et al., 2002). Although controversy exists over the role that different nutritional management strategies (forage vs. concentrate) have on beef product color (Mancini and Hunt, 2005), it is possible that extending the period of time in which steers are permitted to graze pasture with their dams through conventional weaning could have led to the change in muscle color observed by Barker-Neef et al. (2001) and WBSF observed by Schoonmaker et al. (2004) through increasing the glycolytic potential of the ribeye. This theory, however, remains to be proven experimentally.

No reports could be found that compared trained or un-trained consumer sensory perception of beef products from EW to CW cattle. Furthermore, the limited number of experiments that have evaluated the effects of early weaning on physical beef quality characteristics raises awareness to the need for additional research in this field.
Effects of early weaning on calf health

Arthington et al. (2003) reported that ceruloplasmin and haptoglobin, two of the major proteins involved in the acute-phase of an immune response (Baumann and Gauldie, 1994) that are relatively reliable markers of stress in cattle (Conner et al., 1988; Godson et al., 1996; Eckersall, 2000), are elevated in CW beef calves throughout the weaning, commingling and transportation processes. Additionally, the level of these proteins, when measured upon feedlot arrival, is positively related to the incidence of morbidity in finishing cattle (Carter et al., 2002; Berry et al., 2004).

More recently, Arthington et al. (2005) reported a lower level of plasma ceruloplasmin and haptoglobin concentrations of EW compared to CW steers throughout the first 28 d following feedlot arrival, which were both inversely related to ADG of CW, but not EW steers. Plasma ceruloplasmin and haptoglobin concentrations of steers included in this experiment explained a substantial portion of the variation in ADG for CW steers (59 and 40 %, respectively), but only a minimal portion for EW steers (21 and 10 %, respectively). Other authors reported a similar reduction in plasma ceruloplasmin and haptoglobin upon arrival to the feedlot for CW calves that were previously weaned and underwent a 42-d preconditioning period prior to shipment (Step et al., 2008). In addition to reporting similar results to Arthington et al. (2005) for acute-phase protein concentrations, Arthington et al. (2008) also reported approximately a 10 % increase in DM intake, a 37 % increase in ADG, as well as a 30 % increase in G:F over a 29-d feedlot receiving period after a 1600-km shipment for steers that were EW when compared to CW contemporaries. A commonality that early weaning and preconditioning share is familiarity to feed and the feeding environment, as the feed intake of
cattle that have been exposed to bunk-feeding upon arrival to the feedlot is generally greater than cattle that have not been preconditioned (Hutcheson and Cole, 1986).

Myers et al. (1999a) reported a 91% reduction in the overall incidence of respiratory morbidity for EW steers when contrasted against the average of CW steers that were either creep-fed or remained unsupplemented prior to weaning and underwent similar vaccination strategies. Additionally, these authors reported only a small incidence of digestive morbidity (7%) that did not differ between calves weaned at 90 or 215 d of age (Myers et al., 1999a). Based upon these results, it is possible that the reduced incidence of respiratory disease observed for EW calves is a function of increased dry matter intake upon arrival to the feedlot, an enhanced immune system, or some combination of the two.

Smith et al. (2003) reported that steers that were EW at 4 mo of age displayed more distress associated with weaning than their contemporaries that were CW at 7 mo of age. It is possible that the distress associated with early weaning, which typically does not coincide with extensive commingling and transportation across great distances, enhances the ability of EW steers to manage stress later in life. Alternatively, the fact that early weaning does not typically coincide with the aforementioned factors may simply result in a lower degree of stress during commingling and transport. The exact physiological mechanism responsible for these effects, however, remains to be determined. Nonetheless, these results suggest that early weaning enhances the ability of cattle to handle the stress commonly associated with commingling, transportation and the feedlot environment, and that early weaning can be utilized as a viable preconditioning program.
Effects of early weaning on finishing feed intake and efficiency of the calf

Based upon the aforementioned presence of post-weaning compensatory growth that has been observed for CW calves, it seems plausible to assume that this increase in post-weaning growth is a function of elevations in both feed intake and efficiency; two traits that are often considered to be the major physiological mechanisms that drive compensatory growth. Interestingly, however, conflicting reports exist related to the effects of early weaning on finishing average daily feed intake (ADFI) and gross unadjusted feed efficiency (G:F).

Although various researchers have reported no effects of early weaning on finishing ADFI (Lusby et al., 1990; Meyer et al., 2005; Scheffler et al., 2014) or G:F (Lusby et al., 1990; Myers et al., 1999c; Schoonmaker et al., 2004; Arthington et al., 2005), other researchers have reported a reduction (Miller et al., 1991; Myers et al., 1999a; Barker-Neef et al., 2001). Authors who reported reductions in ADFI also reported elevations in G:F for EW steers that ranged from 10 to 15% over their contemporaries (Myers et al., 1999a; Barker-Neef et al., 2001), while Arthington et al. (2005), also reported a 12% elevation in overall G:F during the feedlot phase for EW calves without affecting finishing ADFI. In the experiment conducted by Arthington et al. (2005), EW steers grazed annual ryegrass (*Lolium multiflorum*) followed by perennial stargrass (*Cynodon nlemfuensis*) pasture and were limit-fed concentrate at a rate of 1.0% of BW per d for approximately 215 d while CW calves remained unsupplemented with their dams until being weaned. All steers were then commingled and transported to a feedlot at approximately 300 d of age. In contrast to the findings of the majority of other experiments, EW steers were 18% lighter upon feedlot arrival, suggesting that a portion of the improvement in feed efficiency was likely a function of compensatory growth that was independent of gut fill, as previous nutrient restriction has been shown to reduce NE\textsubscript{g} requirements following re-alimentation to a
higher plain of nutrition (Carstens et al., 1991). Nonetheless, the observations of Myers et al. (1999a) and Barker-Neef et al. (2001) suggest that early weaning results in physiological changes that lead to improvements in finishing feed efficiency.

Although ratio-based measurements such as G:F are considered to be the least labor intensive methods of evaluating feed efficiency, concern of their utility has historically existed due to potentially confounding relationships that exist between feed consumption, and both weight gain and body size (Koch et al., 1963). Variation attributed to these relationships makes the utilization of ratio-based measurements of feed efficiency problematic from a research perspective, particularly for experiments that involve a relatively small sample population. Based upon this concept, it is possible that variation contributed by body size, growth potential and body composition were confounding factors that prevented some researchers from detecting differences in ADFI and G:F, particularly in experiments where BW upon feedlot arrival differed between EW and CW cattle.

In order to account for the potentially confounding variation in feed efficiency that can be attributed to weight gain and body size, Koch et al. (1963) proposed an alternative measurement of feed efficiency that is commonly referred to as residual feed intake (RFI). In calculating RFI, regression of observed ADFI against ADG and average body size during a feed intake measurement period results in the generation of a regression equation that predicts feed intake after accounting for the variation that can be attributed to these traits. The resulting residual value, or the difference between observed and predicted ADFI, provides a measurement of relative feed efficiency within a contemporary group. Due to the nature of its calculation, RFI is a measurement that can be utilized to evaluate feed efficiency independently of growth potential and body size, as well as any additional factors that are utilized in the regression equation, and
could be assumed to be conversely related to true energy requirements for maintenance. Thus, a reduction in RFI would be consistent with an animal consuming less feed at a standard body size and rate of growth, making the animal more efficient.

Barker-Neef et al. (2001) described that EW steers require less energy for maintenance than CW steers throughout finishing, potentially as a result of altered nutrient partitioning, as these authors observed an increase in G:F that was observed in light of a reduction in ADFI. Although not measured by these authors, this would be consistent with an effect on RFI. Heat production associated with metabolic processes, body composition and physical activity accounts for 73% of the variation in RFI (Herd and Arthur, 2009), and is considered to be the major contributor to the energetic cost of maintenance. Ferrell and Jenkins (1998a, b) reported a positive exponential relationship between ME intake and heat production of finishing steers. Based upon this relationship, Herd et al. (2004) hypothesized that cattle with relatively low RFI expend less energy toward heat production, resulting in lower maintenance energy requirements. Although not statistically significant, Wolcott et al. (2010) reported a numerically lower RFI for EW Australian Shorthorn steers when compared to CW contemporaries. However no other reports could be found that evaluated the effect of early weaning on RFI.

Baldwin et al. (1980) reported that the heart, liver and digestive tract are responsible for approximately 39% of the heat production at maintenance for non-lactating cattle, and hypothesized that an increase in nutrient consumption without a corresponding increase in mass of these organs could result in a 10 to 30% improvement in feed efficiency. Alternatively, this could be interpreted to mean that a reduction in mass of these organs without a corresponding reduction in feed consumption would result in a similar improvement in efficiency.
Various authors have reported effects of grouping cattle for RFI on the mass of individual visceral organs. Classification of cattle as low vs. high RFI has corresponded with 8 to 12% reductions in the mass of the liver (Basarab et al., 2003), kidneys (Bonilha et al., 2013) and reticulorumen (Fitzsimons et al., 2014). Reticuloruminal mass accounted for 4% of the variation in feed intake, and RFI increased by 1 kg for each 1-kg increase in mass of these organs (Fitzsimons et al., 2014). However, Mader et al. (2009) and Gomes et al. (2012) reported no differences in individual visceral organ mass of cattle classified as having a low vs. high RFI. Although further research is warranted to determine relationships between visceral organ mass and RFI or other measurements of feed efficiency, it is plausible to conclude that the role that the mass of individual organs play in efficiency may vary widely across cattle populations, and thus be impacted by a number of factors that have yet to be determined.

Sainz and Bentley (1997) provided evidence that feed restriction during the growing phase increased the mass of the liver and intestines of finished cattle. If the same is true for CW steers that remain unsupplemented prior to weaning while EW steers consume concentrate ad libitum, it is likely that an increase in energy required to support an increased visceral organ mass during the finishing phase (i.e. altered nutrient partitioning) could result in reduced feed efficiency of cattle that are limited nutritionally during the growing phase. Additionally, the related differences in visceral organ mass could potentially impact the digestion, absorption and utilization of nutrients.

**Effects of early weaning on cow/calf efficiency and economics**

Another area of interest that has received considerable attention by researchers has been the effects of early weaning on overall efficiency of cow/calf production systems. Peterson et al.
(1987) reported that dams of fall-born EW calves consumed 45 % less TDN from hay than dams of CW calves when fed in a dry lot between the time of early and conventional weaning. In this experiment, early weaning resulted in a 43 % improvement in overall feed efficiency of the cow/calf pair. In support of these results, Llewellyn et al. (2013) reported that early weaning reduced the amount of supplement required by spring-calving beef cows throughout the winter for cows grazing low-quality dormant native range.

Conflicting results exist regarding the economic benefits of early weaning. Early weaning increased the breakeven for a cow/calf pair to an extent great enough to reduce net income of production systems that marketed calves at weaning (Mulliniks et al., 2013), or retained ownership throughout finishing (Story et al., 2000; Barker-Neef et al., 2001; Shike et al., 2007; Meteer et al., 2013). It is important to note, however, that the majority of these latter reports were for calves born in the spring, and did not account for the reduction in feed resources required to support the dam, and the major factor that increased the break-even was supplemental post-weaning feed for EW calves.

While forage abundance throughout lactation is often sufficient for spring-calving herds, times of extended drought often require supplemental feeding of the cow prior to weaning. When evaluated as a drought mitigation strategy, early weaning calves at 90 d of age resulted in a greater bio-economic model-simulated profit margin than supplementing cow/calf pairs during times of forage inadequacy, primarily due to a combination of decreased feed resource requirements to support the pair and enhanced efficiency of the weaned calf (Kruse et al., 2007). Furthermore, fall-calving cow/calf producers often exist in production settings that require a greater level of supplemented feed, indicating that early weaning may be a more advantageous nutritional management strategy when implemented in fall-calving herds.
Although improving efficiency is a priority, improvements in efficiency must be met with an economic benefit in order for a management strategy to be utilized responsibly by beef cattle producers. Based upon this fundamental concept, and the conclusions of previous authors, early weaning is not advisable as a routine management strategy for all cow/calf producers. However, early weaning holds utility as a management practice that can be utilized strategically by cow/calf producers to enhance profitability and production efficiency during times of prolonged drought, and for producers that are required to provide dams with relatively high levels of supplemental feeds throughout lactation. Furthermore, these strategies likely hold the greatest utility for producers that develop their own replacement heifers, as well as producers that retain ownership of cattle throughout finishing.

Conclusion

Based upon collective interpretation of the results of this review of relevant literature, early weaning is an alternative management strategy that has the ability to positively affect both the cow/calf and feedlot sectors of the beef industry. Early weaning typically improves reproductive performance and decreases feed resource requirements of the cow herd. Independent of these improvements, EW calves generally grow faster between the times of early and conventional weaning when managed under a high plane of nutrition, however sacrifice the advantages in compensatory growth that are often observed for their CW contemporaries. Early weaned calves are also better equipped to handle the stressors incurred throughout the various proceeding management phases, potentially due to an enhanced immune system. Additionally, early weaning generally results in an elevation in carcass MS when EW cattle are harvested at a common SFT-based endpoint as CW contemporaries. However conflicting reports exist
throughout the literature regarding the effects of early weaning on finishing feed efficiency, potentially due to the confounding effects of body size and growth potential on feed intake. Furthermore, a void in the literature exists related to the effects of early weaning on meat quality and consumer satisfaction. In order to fill this void, a series of experiments was conducted to evaluate the effects of early weaning on finishing feed efficiency, marbling development, and beef product quality.

**Literature cited**


Chapter II: Effects of early weaning on finishing feed efficiency and carcass traits of beef steers

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ABSTRACT
Early weaning followed by a short period of energy supplementation and pasture backgrounding prior to finishing increases carcass marbling score (MS) of beef cattle, potentially through metabolic imprinting. To further evaluate these effects, a 2-yr experiment was conducted that included Angus-sired steers (n = 90) born in the fall and spring. Steers were randomly assigned to one of two weaning treatments [early weaned (EW; weaned at an average age of 111 d) or conventionally weaned (CW; weaned at an average age of 215 d)]. Following weaning, EW steers were fed a concentrate-based ration ad libitum for an average of 104 d prior to commingling and pasture backgrounding with CW steers for an average of 153 d. Steers were then finished for an average of 121 d at one of two feedlots and harvested in groups upon reaching a common ultrasound-estimated 12th-rib subcutaneous fat thickness (SFT) of 1.0 to 1.2 cm. Un-shrunk BW was measured at 28 d intervals throughout the experiment, and individual finishing feed intake was measured daily for steers born in year 1. Observed ADFI expressed in kg of DM and Mcal of NEg was regressed against average BW^{0.75}, ADG and average SFT during the measurement period, as well as season of birth ($R^2 = 0.79$; $P < 0.0001$ and $R^2 = 0.81$; $P < 0.0001$, respectively) to predict ADFI. Residual feed intake (RFI) was calculated as the difference between observed and predicted ADFI. Carcasses were weighed immediately following harvest, chilled, and evaluated to measure SFT and ribeye area (REA), estimate MS and KPH, and calculate dressing percent (DP) and USDA yield grade (YG). Fixed interaction
and main effects of treatment, season of birth and year of birth were determined via ANOVA. Although a series of interactions ($P < 0.05$) that can be attributed to environmental factors was observed for BW and ADG measured at various time points throughout the experiment, EW steers had a lower RFI when expressed in kg of DM ($P < 0.001$) and Mcal of NE$_g$ ($P < 0.001$), along with greater carcass MS ($P < 0.01$) when compared to CW steers harvested at a similar ($P > 0.10$) SFT-based endpoint. Collectively, these results provide additional evidence that the management strategies reported herein are capable of decreasing RFI and increasing carcass MS, potentially through metabolic imprinting.

**INTRODUCTION**

Over the past few decades, the price structure of the U.S. beef industry has evolved from a traditional commodity-based market to a more quality grade-based retail market. Marbling, or the visual representation of intramuscular fat (IMF) within a beef carcass, is the primary physical factor used to determine USDA quality grade. Additionally, increased competition for feed resources and volatility in climate patterns has placed greater pressure on beef cattle producers to seek alternative management strategies that enhance the efficiency of beef production. Postnatal metabolic function (Long et al., 2010), tissue development (Du et al., 2010; Long et al., 2012b), growth performance (Corah et al., 1975; Funston et al., 2010; Long et al., 2012b) and carcass traits (Stalker et al., 2006; Larson et al., 2009; Underwood et al., 2010) of beef cattle are impacted by maternal nutrition during gestation. Although the majority of these efforts have focused on prenatal, rather than postnatal nutritional manipulation of cattle growth and development, Du et al. (2010) hypothesized that the critical window for enhancing marbling development is between 150 and 250 d of age. Initial work conducted by Scheffler et al. (2014)
identified the ability of an early postnatal period of energy supplementation and accelerated
growth to enhance carcass marbling when followed by pasture backgroundering and feedlot finishing, potentially through metabolic imprinting events. Others reported reduced finishing ADFI and improved gross unadjusted feed efficiency in EW calves (Myers et al., 1999b; Barker-Neef et al., 2001). Based upon these findings, an experiment was conducted to evaluate the ability of an early energy supplementation and accelerated growth phase to modulate beef cattle physiology in order to improve finishing feed efficiency and enhance carcass marbling.

MATERIALS AND METHODS
All procedures reported herein were approved by the Virginia Tech Institutional Animal Care and Use Committee.

Cattle

Angus-sired steer progeny (n = 90) from the Virginia Tech commercial beef herd born in the fall and spring of two years were used in this experiment. Male progeny from each of four calving seasons were managed within contemporary groups that were defined by season and year of birth. Contemporary groups are further described in Table 1. Calves were sired by one of sixteen commercially available AI sires. All calves were castrated within 24 h of birth and received initial 7-way clostridial (Vision 7; Merck and Co., Inc., White House Station, NJ 08889) and modified-live virus respiratory disease complex (Bovi Shield Gold FP5 VL5; Zoetis, Florham Park, NJ 07932) vaccinations 14 d prior to the time of early weaning, which were repeated 28 d post initial vaccination. Calves were treated topically with doramectin (Dectomax; Zoetis, Florham Park, NJ 07932) for prevention and control of internal and external parasites at
the time of conventional weaning, and remained un-implanted throughout the duration of the experiment.

Management

Previously unsupplemented steers were stratified by BW before being randomly assigned to one of two treatment groups: EW or CW. Early weaned steers were weaned at an average of 111 d of age (Table 1) and provided *ad libitum* access to a concentrate-based ration (Table 2) and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d. Early weaned steers were initially offered the concentrate-portion of the ration in the form of a commercially-manufactured calf starter (Southern States Cooperative, Richmond, VA 23294), and were transitioned to a custom-blended concentrate after 5 d. Concentrate formulations were adjusted at 21-d intervals to decrease CP content by replacing soybean meal with cracked corn and wheat middlings. Throughout this period, CW steers remained unsupplemented with their dams until being weaned at an average of 215 d of age (Table 1).

Following conventional weaning, EW and CW steers were commingled and backgrounded on annual and perennial forages in a grazing setting for an average of 153 d. Steers were provided *ad libitum* access to corn silage throughout the final 21 d of the backgrounding phase, which initiated adaptation to the finishing ration. Upon completion of the backgrounding phase, steers were transported to feedlots at either the Shenandoah Valley Agricultural Research and Extension Center located in Raphine, VA (spring and fall of year 1) or the Virginia Tech Beef Center located in Blacksburg, VA (spring and fall of year 2) for finishing. Steers fed at the Shenandoah Valley Agricultural Research and Extension Center were stratified by treatment, sire and BW before being randomly assigned to one of four pens. All steers
finished at the Virginia Tech Beef Center were fed within a single pen. Steers were adapted to a concentrate- and corn silage-based finishing ration (Tables 2 and 3) in a step-wise fashion by replacing corn silage with concentrate over a period of 21 d that consisted of three additional steps. Fresh total mixed ration (TMR) was prepared daily by blending a pre-manufactured concentrate pellet (Table 2) with corn silage immediately prior to offering, which occurred once daily between the hours of 0800 and 1000 at an initial rate of 14 kg per steer per d. Offerings were adjusted daily to achieve refusals of approximately 5%. Steers were finished for an average of 121 d before being harvested in groups at one of two abattoirs (J. W. Treuth and Sons Inc., Baltimore, MD 21228, or the Virginia Tech Meat Science Center, Blacksburg, VA 24061) upon reaching an ultrasound-estimated common SFT endpoint of approximately 1.0 to 1.2 cm.

**Ration composition**

Bi-weekly concentrate and hay samples collected throughout the early dry-lot feeding period, as well as corn silage, concentrate pellet and TMR samples collected throughout the finishing phase were frozen and stored at -20 °C prior to being thawed and combined to form representative composites within contemporary group. Samples were analyzed to determine nutrient content by an independent laboratory (Dairy One, Ithaca, NY 14850).

**BW and ADG**

Un-shrunk BW was measured within 24 h of birth, at 28 ± 7 d intervals throughout the remainder of the experiment, and at the completion of each management phase. Total and within management-phase un-shrunk BW gain was calculated by difference from BW collected at the initiation and completion of each production phase and used to calculate total and within management-phase ADG.
Ultrasound

Transdermal body compositional ultrasound images were collected at the transition from each management phase for steers born in the spring and fall of year 1. In order to facilitate image collection, a 36 cm x 36 cm area of hide lateral to and projecting cranially from the ventral end of the 13\textsuperscript{th} rib was clipped, brushed and coated with soybean oil prior to image collection. Images were collected using an Aloka 500V real-time ultrasound machine equipped with a 17.2-cm, 3.5-MHz linear transducer (Hitachi Aloka Medical America, Inc., Wallingford, CT 06492), then processed and interpreted by an independent centralized ultrasound processing laboratory (Walter & Associates, LLC, Ames, IA 50010) in order to estimate REA, SFT and percent IMF. All steers, regardless of season and year of birth, were ultrasounded at approximately 70 d following arrival to the feedlot in order to measure 12\textsuperscript{th}-rib SFT in real-time to stage harvest groups. Efforts were made to harvest steers in groups at a common ultrasound-estimated SFT endpoint of 1.0 to 1.2 cm.

Carcass

Trimmed and washed HCW was measured immediately following harvest and prior to carcasses being placed in a cooler (2.8 °C), and used to calculate DP. Upon completion of a 24-h chilling period, the left side of each carcass was ribbed between the 12\textsuperscript{th} and 13\textsuperscript{th} costae to facilitate carcass data collection. Carcasses were evaluated by two trained analysts for measurement of SFT and REA, and estimation of MS and KPH. Measurements were averaged across analysts and used to calculate YG.

Finishing feed intake and feed efficiency

Daily individual feed intake was measured for steers born in the spring and fall of year 1 using a Calan-Broadbent feed intake measurement system (American Calan, Inc., Northwood,
Steeers were trained to individual Calan gates, with training initiated upon arrival to the feedlot and completed prior to or at the time of transition to the final finishing ration adaptation step. Initiation of the daily individual feed intake measurement period corresponded with transition to the final finishing ration, and ended the d preceding harvest. Duration of the daily feed intake measurement period ranged from 67 to 118 d for steers born in the spring, and 77 to 106 d for steers born in the fall. Offered TMR and refusals were weighed daily to the nearest 0.05 kg. Daily as-fed TMR intake was calculated by difference of offerings and refusals. As-fed ADFI was calculated by dividing the sum of as-fed TMR intake observations by the duration of the intake data collection period expressed in d. Average daily feed intake was expressed in units of DM, NE\textsubscript{m} and NE\textsubscript{g} by multiplying ADFI by the respective unit.

Un-shrunk BW was measured at the onset (initial BW) and completion (final BW) of the feed intake measurement period, and used to calculate average un-shrunk BW and BW\textsuperscript{0.75}. Average daily gain was calculated by dividing the difference of final BW and initial BW by the duration of the feed intake measurement period in d. In order to calculate individual average NE\textsubscript{m} requirement during the feed intake measurement period, individual average empty BW (EBW) was calculated as reported by Williams et al. (1992):

$$\text{EBW} = (\text{un-shrunk BW} / 1.09) - 4.$$ 

Individual average NE\textsubscript{m} requirement during the feed intake measurement period was then calculated as reported by the NRC (1996):

$$\text{NE}_m = 0.077 \text{ Mcal} / \text{EBW}^{0.75}.$$ 

Individual ADFI expressed in NE\textsubscript{m} equivalents was calculated using the following equation:

$$\text{NE}_m \text{ intake equivalents} = \text{ADFI} / (0.077 \text{ Mcal} / \text{EBW}^{0.75}),$$
where ADFI is expressed in Mcal of NE$_m$. Individual observed ADFI in excess of calculated NE$_m$ requirement, termed residual NE$_m$ intake, was calculated using the following equation:

$$\text{Residual NE}_m \text{ intake} = \text{ADFI} - (0.077 \text{ Mcal} / \text{EBW}^{0.75}),$$

where ADFI is expressed in Mcal of NE$_m$.

Gross unadjusted feed efficiency was expressed as the ratio of ADG in kg to ADFI in kg of DM. Residual NE$_m$ efficiency was calculated using the following equation:

$$\text{Residual NE}_m \text{ efficiency} = \frac{\text{ADG}}{\text{ADFI} - (0.077 \text{ Mcal} / \text{EBW}^{0.75})},$$

where ADG and ADFI were expressed in kg and Mcal of NE$_m$, respectively.

Observed individual ADFI was regressed against average BW$^{0.75}$, ADG and average SFT (calculated as the average of ultrasound-estimated SFT upon completion of the backgrounding phase and carcass SFT) during the feed intake measurement period, as well as season of birth, via the Fit Model procedure of JMP Pro v.11 (SAS Institute Inc., Cary, NC 27513) to predict ADFI in kg of DM and Mcal of NE$_m$. The linear regression model was:

$$Y_j = \beta_0 + \beta_1 \text{BW}^{0.75}_j + \beta_2 \text{ADG}_j + \beta_3 \text{SFT}_j + \beta_4 \text{SEA}_j + e_j,$$

where $Y_j$ represents observed ADFI of the $j$th animal, $\beta_0$ represents the regression intercept, $\beta_1 \text{BW}^{0.75}_j$ represents the partial regression coefficient for average BW$^{0.75}$ of the $j$th steer, $\beta_2 \text{ADG}_j$ represents the partial regression coefficient for ADG of the $j$th steer, $\beta_3 \text{SFT}_j$ represents the partial regression coefficient for average SFT of the $j$th steer, $\beta_4 \text{SEA}_j$ represents the partial regression coefficient of the $j$th season of birth, and $e_j$ represents the random error associated with the $j$th steer. Residual feed intake, a non-ratio-based measurement of feed efficiency, was calculated as the difference between observed and predicted ADFI expressed in kg of DM and Mcal of NE$_g$. 

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Statistical analyses

All statistical analyses were conducted using JMP Pro, and steer was considered the experimental unit. The Factor Screening procedure was used to identify potential explanatory variables not of direct primary interest to the hypothesis that explained a significant ($P < 0.05$) portion of the variation in one or more response variables. Factors screened included parity of dam nested within year of birth, sire nested within season of birth, and age at the time of measurement for each individual response variable, as well as feedlot pen nested within season of birth for carcass, feed intake and feed efficiency response variables. Based upon the results of the initial factor screening, sire nested within season of birth and age at the time of measurement for a respective response variable explained a significant ($P < 0.05$) portion of the variation in one or more response variables, and were initially included as a blocking factor and covariate, respectively, in subsequent statistical analyses.

Analysis of variance was conducted via the Fit Model procedure to determine interaction and main effects of treatment, season of birth and year of birth for BW, ADG and carcass response variables. Treatment was considered a fixed effect, and season of birth and year of birth were considered random effects. The initial ANOVA model for ultrasound response variables, as well as response variables for finishing feed intake, BW, ADG and feed efficiency during the feed intake measurement period for steers born in the spring and fall of year 1 consisted of interaction and main effects of treatment and season of birth, which were considered fixed and random effects, respectively. Sire nested within season of birth and age at the time of measurement were used as blocking factors and covariates, respectively, in all initial statistical models. Additionally, carcass SFT was included as a covariate for HCW and MS, and HCW was included as a covariate for REA.
Resulting data were initially evaluated to verify equality of variance and normality by plotting residual by predicted values for each response variable. Although negatively skewed data were observed for carcass REA and MS, transformations were unsuccessful at achieving normality. As such, untransformed data were analyzed. Plots of residual by predicted values were also used to visually detect potential outliers. No more than three observations within each response variable were identified as outliers and subsequently removed from further analysis.

Final statistical models were reduced in a step-wise fashion to remove statistically insignificant interaction and main effects. Least square means for statistically significant interaction effects were separated using the Tukey-Kramer honestly significant difference method, and individual $P$-values were observed through the generation of ordered difference reports.

RESULTS AND DISCUSSION

Ration composition

Ingredient and nutrient composition of the final concentrate offered to EW steers during the early dry-lot feeding period and the concentrate pellet offered as a component of the finishing TMR for all steers are reported as a respective average across season and year of birth in Table 2, as formulations remained consistent throughout the duration of the experiment. Component and nutrient composition of the final finishing TMR fed to each contemporary group at the completion of the adaptation period and throughout the remainder of the feed intake measurement period are reported in Table 3, as source of corn silage differed for each contemporary group.
Least square means of treatment, season of birth and year of birth for BW and ADG are reported in Table 4. Steers born in the spring tended \((P = 0.06)\) to be heavier at birth than steers born in the fall, and steers born in year 2 were heavier \((P < 0.001)\) at the time of early weaning than steers born in year 1, suggesting that environmental influences may have impacted the nutritional status of dams across season of birth and year of birth. Although treatment by season \((P < 0.01)\), treatment by year \((P < 0.0001)\), and season by year \((P < 0.0001)\) interactions existed for BW at the time of conventional weaning, EW steers were consistently heavier upon completion of the early concentrate feeding period than CW steers that remained with their dams within the treatment by season and treatment by year interactions, due to the elevated plane of nutrition for EW steers. These results are consistent with those reported by other researchers that provided EW steers with \textit{ad libitum} access to concentrate following early weaning while CW steers remained unsupplemented with their dams (Lusby et al., 1990; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Meyer et al., 2005; Waterman et al., 2012; Scheffler et al., 2014).

Season by year \((P < 0.01)\) and treatment by year \((P < 0.05)\) interactions existed for BW upon completion of the backgrounding phase. Although forage quality during the backgrounding phase was not measured, these interactions could be the result of seasonal variation in forage quality, as steers born in the fall were backgrounded during the late spring and summer, and steers born in the spring were backgrounded during the late fall and winter. Additionally, a three-way interaction between treatment, season of birth and year of birth was observed for finished BW \((P < 0.0001)\). Conventionally weaned steers born in the fall of year 2 were the heaviest \((P < 0.05)\) upon completion of the finishing phase and differed from all other
three-way combinations, while EW steers born in the fall of year 2 were heavier \((P < 0.01)\) than EW steers born in the spring of year 1. This was likely a function of numeric differences in BW that were observed upon completion of the backgrounding phase, and could further be attributed to environmental differences associated with the assumed variation in forage quality.

A three-way interaction between treatment, season of birth and year of birth existed for ADG between birth and the time of early weaning \((P < 0.05)\), driven by a relatively low ADG of EW steers born in the spring of year 1, and relatively high ADG of EW steers born in the spring of year 2, which differed significantly from each other \((P < 0.05)\), but not from other combinations \((P \geq 0.23)\). A three-way interaction between treatment, season of birth and year of birth also existed for ADG between the time of early and conventional weaning \((P < 0.01)\), driven by a tendency for a difference \((P = 0.08)\) in ADG of EW and CW steers born in the spring of year 2. The interaction may be the result of an elevated level of growth between the time of birth and early weaning, suggesting a difference in nutritional status of the dams that could be attributed to environmental conditions. Within this interaction, ADG between the times of early and conventional weaning was greater \((P < 0.0001)\) for EW than CW steers for all other season of birth by year of birth combinations, and was numerically greater for EW than CW steers, regardless of season of birth or year of birth. Nayananjalie et al. (2015a) reported an increase in the phosphorylation ratios of ribosomal protein S6 and S6 kinase 1 for EW steers managed under similar conditions, which independently explained 25 and 22 % of the variation in ADG, respectively. Increased phosphorylation of these signaling proteins would be consistent with the results that were observed for ADG between the times of early and conventional weaning.

Two-way interactions between treatment and season \((P < 0.0001)\), treatment and year \((P < 0.001)\), and season and year \((P < 0.0001)\) existed for ADG during the backgrounding phase.
Although these interactions were likely driven by environmental variation associated with season of birth and year of birth, backgrounding ADG was consistently lower for EW than CW steers within the treatment by season and treatment by year interactions. The abrupt transition from receiving concentrate *ad libitum* in a dry-lot setting to grazing in a pasture setting, or the presence of compensatory growth that existed during the early dry-lot feeding period for EW steers may account for these differences.

A three-way interaction between treatment, season of birth and year of birth existed for finishing ADG (*P* < 0.05). Although this three-way interaction did not exist for BW upon completion of the backgrounding phase, BW of EW and CW steers born in the spring of year 2 were numerically lower than all other three-way combinations, indicating that this interaction may have been the result of compensatory growth that occurred upon acclimation to the finishing ration.

*Ultrasound*

Least square means of treatment and season of birth for ultrasound-estimated SFT, REA and IMF of steers born in year 1 are reported in Table 5. Unexpectedly, SFT tended to be greater for CW than EW steers at the time of early weaning (*P* = 0.07), but was greater for EW than CW steers at the time of conventional weaning (*P* < 0.0001). Upon completion of the backgrounding phase, SFT remained greater for EW than CW steers (*P* < 0.05), indicating retention throughout the grazing period.

Ultrasound-estimated REA of EW steers born in the spring was smaller at the time of early weaning than EW steers born in the fall (*P* < 0.0001), CW steers born in the spring (*P* < 0.01) and CW steers born in the fall (*P* < 0.001). At the time of conventional weaning, REA was larger for EW than CW steers (*P* < 0.001) and tended to be larger for steers born in the fall than
Similar to the results observed for ADG, the greater REA of EW steers that was observed upon completion of the early dry lot feeding period was likely a function of increased phosphorylation of signaling proteins involved in muscle hypertrophy that were reported by Nayananjalie et al. (2015a).

Additionally, IMF was greater ($P < 0.01$) for CW steers born in the fall than all other treatment by season of birth combinations at the time of conventional weaning. This indicates that the combination of early weaning and concentrate feeding did not enhance IMF of EW steers upon completion of the early dry lot feeding period. Although consistent with results of other researchers who reported elevations in ultrasound-estimated SFT and LMA (Schoonmaker et al., 2004; Meyer et al., 2005), this is inconsistent with the higher level of IMF reported by Schoonmaker et al. (2004) at the time of conventional weaning for steers that were EW and fed concentrate ad libitum until the time of conventional weaning. However it is possible that these inconsistencies are a function of limitations associated with current carcass ultrasound estimations.

Upon completion of the backgrounding phase, REA was larger for steers born in the fall than spring ($P < 0.001$), but did not differ between treatments ($P = 0.36$). Although a treatment by season of birth interaction existed for IMF upon completion of the backgrounding phase ($P < 0.05$), post-grazing IMF did not differ ($P = 0.50$) between EW and CW steers. This suggests an enhanced ability of EW steers to accrete IMF following the early dry-lot feeding period that could have been the result of imprinted physiological changes that led to the enhancement in IMF development that was observed during the backgrounding phase. No previous reports could be found that compared ultrasound-estimated SFT, REA or IMF of EW to CW steers at the initiation or completion of each production phase for experiments that included a backgrounding
phase prior to finishing. Although the elevation in SFT and REA of EW steers at the time of conventional weaning can most likely be attributed to enhanced nutritional status, the lack of an elevation in IMF of EW compared to CW steers at the time of conventional weaning supports the argument that any observed elevation in carcass MS of EW steers could be attributed to metabolic imprinting events that occurred during the early dry-lot feeding period.

**Carcass**

Least square means of treatment, season of birth and year of birth for carcass measurements are reported in Table 6. Although efforts to harvest steers at a common SFT across years 1 and 2 were unsuccessful \((P < 0.001)\), EW and CW steers, as well as steers born in the spring and fall were harvested at a similar SFT \((P = 0.49\) and \(P = 0.38\), respectively), indicating that these steers were harvested at a common endpoint.

Three-way interactions between treatment, season of birth and year of birth existed for HCW \((P < 0.01)\) and REA \((P < 0.05)\). Although the complexity of these interactions makes interpretation difficult, these interactions follow patterns similar, but not identical to that which was observed for finished BW, indicating that they could have been the result of confounding variation contributed by BW and environmental influences that existed across season of birth and year of birth that were not accounted for by the ANOVA model. Although not analyzed statistically, means within treatment, season of birth and year of birth combinations suggest that a relationship between HCW and SFT existed, as HCW appeared to be greater for combinations that were harvested at a greater average SFT. However the inclusion of SFT as a covariate for HCW and HCW as a covariate for REA did not explain the variation across combinations that resulted in the existence of these complex interactions. Although Schoonmaker et al. (2004) reported a smaller LMA of carcasses from EW than CW steers, potentially as a result of the
lower HCW of EW steers, the lack of an effect of early weaning on carcass REA in the present experiment is consistent with the results reported by other researchers (Harvey et al., 1975; Lusby et al., 1990; Loy et al., 1999; Myers et al., 1999b; Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Arthington et al., 2005; Meyer et al., 2005; Waterman et al., 2012). Additionally, a season of birth by year of birth interaction was observed for DP (P < 0.05), which could have been the result of the confounding interactions associated with HCW and SFT, as DP is positively and linearly related to physiological maturity (May et al., 1992; Bruns et al., 2004). No other two-way interactions were observed for the remaining carcass response variables (P ≥ 0.23), however steers born in year 1 tended to have a higher KPH (P = 0.07) but had a lower YG (P < 0.0001) than steers born in year 2. Harvey et al. (1975) reported a tendency toward decreased KPH and Myers et al. (1999b) reported an elevation in KPH and YG of EW steers. However the low magnitude of the previously reported differences has little to no biological or economic significance. The lack of an effect of early weaning on KPH and YG in the present experiment is consistent with other reports showing no difference between EW and CW calves that remained unsupplemented prior to finishing (Lusby et al., 1990; Loy et al., 1999; Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Waterman et al., 2012), indicating that any elevation in carcass MS would not be at the expense of elevated KPH or YG.

Carcass MS was greater for steers born in year 1 than 2 (P < 0.01). Independent of this effect, MS was greater for EW than CW steers (P < 0.01). When combined with the results reported for ultrasound-estimated IMF upon completion of the backgrounding phase, the 10 % increase in carcass MS observed for EW steers indicates that early weaning, when followed by an early dry-lot feeding period and pasture backgrounding phase immediately prior to finishing
was capable of enhancing IMF development over and beyond that of a conventional weaning. As such, the alternative nutritional management practice reported herein may be a useful tool to metabolically imprint beef cattle for improved marbling development and quality grade. These results are qualitatively consistent with those reported by Scheffler et al. (2014) who also included a backgrounding phase prior to finishing, as well as a number of researchers that finished steers immediately following the time of conventional weaning and completion of the EW feeding period (Loy et al., 1999; Myers et al., 1999b; Meyer et al., 2005; Shike et al., 2007; Waterman et al., 2012). The inconsistent reports of an effect of early weaning on MS may reflect differences in harvest endpoints. Various authors (Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Arthington et al., 2005; Moriel et al., 2014a) fed steers to a target SFT-based harvest endpoint immediately following the time of conventional weaning, which resulted in EW cattle being harvested at a younger age or after being finished for a shorter duration. This is further supported by the elevated degree of ultrasound-estimated SFT that was observed for EW steers upon completion of the early dry-lot feeding period in the present experiment.

Research conducted by Moriel et al. (2014a) provided evidence that early nutritional management strategies similar to those reported herein are capable of enhancing muscle \( PPAR\gamma \) mRNA expression when measured at the completion of the EW feeding period. Although those same authors reported no difference in carcass MS between EW and CW steers, the lack of an effect could have been associated with biological type, as cattle included in the experiment were progeny of at least one parent with \( Bos \ indicus \) genetic influence, and therefore could be assumed to have had a lower genetic propensity for marbling. Additionally, Moisá et al. (2014) reported that expression of the adipogenic master regulatory genes \( CEBP\alpha \) and \( PPAR\gamma \), along
with a number of additional downstream adipogenic and lipogenic genes and enzymes increased soon after the time of weaning for EW steers managed under a similar strategy, but not CW steers. Although gene or enzyme expression was not measured for the steers reported herein, the aforementioned observations of previous authors, when paired with the elevation in ultrasound-estimated IMF that was observed for EW steers upon completion of the backgrounding phase suggests that the enhanced MS of EW steers could have been the result of increased preadipocyte recruitment and lipogenesis throughout the backgrounding and finishing phases, potentially through imprinted upregulation of the CEBPa and PPARγ regulatory network.

Although once thought to exist in a terminally differentiated state, in vitro evidence that mature adipocytes are capable of dedifferentiating to a preadipocyte stage (Fernyhough et al., 2004; Dodson et al., 2005) and redifferentiating to form adipocytes that accumulate lipid (Fernyhough et al., 2007) exists. Early reports of experiments conducted in vitro suggested acetate to be the preferred energy substrate for fatty acid synthesis in bovine visceral (Hanson and Ballard, 1967) and subcutaneous adipose (Hood et al., 1972), and glucose the preferred substrate for triglyceride-glycerol synthesis (Hood et al., 1972). Smith and Crouse (1984) later reported a preference of intramuscular adipocytes for glucose over acetate as an acetyl unit donor for fatty acid synthesis, however interpretation of results reported by Miller et al. (1991) suggest a preference for acetate over glucose as a precursor for fatty acid synthesis by both subcutaneous and intramuscular adipose. This was more recently supported by Nayananjalie et al. (2015b), who reported similar in vivo fractional palmitate synthesis rates from acetate and glucose in visceral, subcutaneous and intramuscular adipose. Increased supply of energy substrates during the early dry-lot feeding period could have enhanced marbling development of EW steers at the cellular level that was not evident in ultrasound-estimated IMF. Thus, it is possible that a portion
of intramuscular adipocytes developed during the early concentrate feeding period of EW steers could have dedifferentiated to a preadipocyte stage in response to a lower plane of nutrition throughout the pasture backgrounding phase, as indicated by ADG. Once acclimated to the final finishing ration, increased supply of energy substrates could have resulted in upregulation of the CEBPα and PPARγ network, resulting in preadipocyte redifferentiation that increased the population of intramuscular adipocytes that was recognized as an increase in carcass MS. Alternatively, advanced early cellular development could have resulted in an increased population of intramuscular adipocytes that were retained throughout the pasture backgrounding phase, and were thus capable of accumulating a greater amount of lipid upon acclimation to the finishing ration. The presence of these specific effects, however, remains to be evaluated, and further research is warranted to determine the underlying physiological mechanism(s) associated with metabolic imprinting events that alter marbling development.

**Finishing feed intake measurement and feed efficiency**

Least square means of treatment and season of birth for BW, BW\(^{0.75}\), ADG and calculated NE\(_m\) requirement during the finishing feed intake measurement period of steers born in year 1 are reported in Table 7. Two-way interactions between treatment and season of birth existed for initial BW (\(P < 0.0001\)), final BW (\(P < 0.0001\)), total BW gain (\(P < 0.05\)), as well as average BW (\(P < 0.01\)) and BW\(^{0.75}\) (\(P < 0.01\)) during the feed intake measurement period. Initial BW was greater for EW steers born in the fall than CW steers born in the spring (\(P < 0.001\)), EW steers born in the spring (\(P < 0.001\)) and CW steers born in the fall (\(P < 0.01\)). Final BW of EW steers born in the fall was greater than EW steers born in the spring (\(P < 0.01\)) and CW steers born in the fall (\(P < 0.05\)), and tended to differ from CW steers born in the spring (\(P = 0.09\)). Total BW gain was greater for CW steers born in the spring than EW steers born in the spring (\(P\)
Expectedly, based upon the results observed for initial and final BW, average BW and BW\(^{0.75}\) was greater for EW steers born in the fall than CW steers born in the fall (\(P < 0.05\) and \(P < 0.05\), respectively), CW steers born in the spring (\(P < 0.05\) and \(P < 0.05\), respectively), and EW steers born in the spring (\(P < 0.001\) and \(P < 0.01\), respectively), which did not differ from one another (\(P \geq 0.70\) and \(P \geq 0.70\), respectively). No two-way interaction (\(P = 0.54\)) or main effects of treatment (\(P = 0.65\)) or season of birth (\(P = 0.11\)) were observed for ADG during the feed intake measurement period. Driven by the interaction between treatment and season of birth that existed for average BW and BW\(^{0.75}\), a two-way interaction between treatment and season of birth existed for calculated NE\(_m\) requirement (\(P < 0.01\)), as EW steers born in the fall had a greater calculated NE\(_m\) requirement than CW steers born in the fall (\(P < 0.05\)), CW steers born in the spring (\(P < 0.05\)), and EW steers born in the spring (\(P = 0.001\)), which did not differ from one another (\(P \geq 0.70\)). These results conflict with those of Barker-Neef et al. (2001) who reported a 20% reduction in NE\(_m\) requirements of EW steers, potentially as a result of the inclusion of an additional growth phase following the initial dry-lot feeding period of EW steers in the present experiment.

Least square means of treatment and season of birth for feed intake and feed efficiency during the finishing feed intake measurement period of steers born in year 1 are reported in Table 8. A two-way interaction between treatment and season of birth existed for observed total feed intake when expressed in kg of DM (\(P < 0.0001\)). Observed total feed intake was lowest for EW steers born in the spring, which differed significantly from all other treatment by season of birth combinations (\(P < 0.0001\)), but did not differ between EW steers born in the fall and CW steers born in the spring and fall (\(P \geq 0.89\)), which was likely a function of the lower calculated NE\(_m\) requirement and finished BW of EW steers born in the spring. This is further supported by the
lack an interaction between treatment and season of birth for ADFI when expressed in kg of DM per d ($P = 0.53$), Mcal of NE$_g$ per d ($P = 0.53$), equivalents of NE$_m$ requirement per d ($P = 0.48$), or residual NE$_m$ intake ($P = 0.53$).

Although unaffected by treatment ($P = 0.25$), a main effect of season of birth existed for observed and predicted ADFI when expressed in kg of DM per d and Mcal of NE$_g$ per d, as steers born in the fall had a greater observed ($P < 0.0001$ and $P < 0.0001$, respectively) and predicted ($P < 0.0001$ and $P < 0.0001$, respectively) ADFI than steers born in the spring. In the present experiment, steers born in the fall were finished during the following fall and winter, while steers born in the spring were finished during the following spring and summer. When combined with lower temperatures throughout the fall and winter when compared to spring and summer, finishing steers in un-bedded, concrete-floored pens likely elevated energetic expenditure for body temperature regulation, which would have resulted in a corresponding increase in observed and predicted ADFI. The lack of an effect of early weaning on observed ADFI during the finishing phase is consistent with those reported by Lusby et al. (1990), Meyer et al. (2005) and Scheffler et al. (2014). Others reported reductions in observed ADFI throughout finishing for EW steers, however these experiments did not include an additional backgrounding or growth phase following the early concentrate feeding period and prior to finishing (Myers et al., 1999b; Barker-Neef et al., 2001). Nonetheless, main effects of treatment and season of birth existed for observed ADFI when expressed in daily equivalents of calculated NE$_m$ requirement, as EW steers had a lower observed ADFI than CW steers ($P < 0.05$), and steers born in the spring had a lower observed ADFI than steers born in the fall ($P < 0.0001$). Similarly, a main effect of season of birth ($P < 0.0001$) and tendency for a main effect of treatment ($P = 0.05$) existed for ADFI when expressed as residual NE$_m$ intake, as steers born in
the fall consumed a greater amount of NE$_{m}$ in excess of their calculated requirement than steers born in the spring ($P < 0.0001$), and EW steers tended to consume less than CW steers ($P = 0.05$). Collectively, these results indicate that early weaning, when followed by an early dry-lot feeding period and pasture backgrounding phase immediately prior to finishing was capable of metabolically imprinting steers for reductions in finishing feed intake that were confounded by variation in BW. This provides additional evidence that individual NE$_{m}$ requirements should be taken into consideration when evaluating feed intake, particularly in experiments involving observations obtained from a relatively small sample population and/or observations obtained from greater than one season or year.

A two-way interaction between treatment and season of birth existed for gross unadjusted feed efficiency ($P < 0.05$), as the ratio of G:F for EW steers born in the fall was lower than EW ($P < 0.001$) and CW ($P < 0.05$) steers born in the spring. Although others reported no effect of early weaning on G:F during the finishing phase (Lusby et al., 1990; Myers et al., 1999c; Schoonmaker et al., 2004; Arthington et al., 2005), Myers et al. (1999b) reported an elevation in G:F for EW steers when contrasted against the average of previously unsupplemented CW and creep-fed CW steers. Additionally, Barker-Neef et al. (2001) reported an elevation in G:F for EW steers when expressed for various time points throughout finishing.

Although a treatment by season of birth interaction did not exist for residual NE$_{m}$ efficiency ($P = 0.88$), a main effect of season of birth and a tendency toward a main effect of treatment was observed. Steers born in the spring required fewer Mcal of NE$_{m}$ per kg of BW gain than steers born in the fall ($P < 0.0001$), providing additional evidence that suggests environmental effects on body temperature regulation. Independent of this effect, EW steers tended to require fewer Mcal of NE$_{m}$ per kg of BW gain than CW steers ($P = 0.05$), which is
consistent with the results of Barker-Neef et al. (2001) who reported that EW steers required less energy for maintenance than CW steers throughout finishing.

Linear regression models fitted to predict ADFI expressed in kg of DM and Mcal of NE\textsubscript{g} included regression intercepts of 0.21 and 0.28, respectively, and partial regression coefficients of 0.06 and 0.08 for average BW\textsuperscript{0.75}, respectively, 2.32 and 2.78 for ADG, respectively, 4.78 and 5.76 for average SFT, respectively, and -0.75 and -1.02, respectively for steers born in the spring, or 0.75 and 1.02, respectively for steers born in the fall, and were capable of explaining a significant and substantial portion of the variation in observed ADFI ($P < 0.0001$; adjusted $R^2 = 0.79$ and $P < 0.0001$; adjusted $R^2 = 0.81$, respectively). No two-way interaction of treatment and season of birth or main effect of season were observed for RFI when expressed in kg of DM per d ($P = 0.13$ and $P = 0.69$, respectively) or Mcal of NE\textsubscript{g} per d ($P = 0.13$ and $P = 0.69$, respectively), as variation attributed to BW, growth potential, body composition and season of birth were removed via regression. After removing this variation, treatment affected RFI, as EW steers had a 0.77 kg and 0.93 Mcal lower ($P < 0.001$ and $P < 0.0001$, respectively) RFI than CW steers when expressed relative to daily DM and NE\textsubscript{g} intake, respectively. When expressed relative to the ADFI that was observed for CW steers, this reduction in RFI represents a 7 % improvement in feed efficiency, suggesting that metabolic imprinting events occurred during the EW feeding period that enhanced finishing feed efficiency. Although not statistically significant, and to a lesser magnitude, Wolcott et al. (2010) reported a numerically lower RFI for EW Australian Shorthorn steers when compared to CW contemporaries. However no other reports could be found that evaluated the effect of early weaning on RFI.

Heat production associated with metabolic processes, body composition and physical activity has been previously reported to account for 73 % of the variation in RFI (Herd and
Arthur, 2009), and is considered to be the major contributor to the energetic cost of maintenance. Ferrell and Jenkins (1998a) reported a positive exponential relationship between ME intake and heat production of finishing steers. Based upon the relationship that exists between feed intake and energetic expenditure for heat production, Herd et al. (2004) hypothesized that cattle with relatively low RFI expend less energy toward heat production, resulting in lower maintenance energy requirements. Based upon the results reported herein, as well as those reported by Barker-Neef et al. (2001) for gross unadjusted feed efficiency, the tendency toward an improvement in residual $\text{NE}_m$ efficiency and improvement in RFI of EW steers may be a function of altered nutrient partitioning, as these data support the notion that EW steers have lower true $\text{NE}_m$ requirements.

Baldwin et al. (1980) reported that the heart, liver and digestive tract are responsible for approximately 39 % of the heat production at maintenance for non-lactating cattle, and hypothesized that an increase in nutrient consumption without a corresponding increase in organ mass could result in a 10 to 30 % improvement in feed efficiency. Sainz and Bentley (1997) provided evidence that feed restriction during the growing phase increased the mass of the liver and intestines for cattle that received ad libitum access to a concentrate-based ration throughout finishing when compared to cattle that were fed a concentrate-based ration ad libitum during the growing phase. Based upon these concepts, an increase in energy required to support increased visceral organ mass during the finishing phase could result in reduced feed efficiency of cattle that are limited nutritionally during the growing phase, as well as impact the digestion, absorption and utilization of nutrients. Reduced visceral organ mass could explain the differences observed in residual $\text{NE}_m$ efficiency and RFI. Nonetheless, further research is necessary to better understand the impact that this alternative early nutritional management
strategy has on visceral organ mass in order to identify the underlying physiological mechanism(s) responsible for the EW improvement in finishing feed efficiency.

**CONCLUSIONS AND IMPLICATIONS**

Collective interpretation of the results reported herein and that of other researchers suggest that a combination of early weaning and a short *ad libitum* concentrate feeding period prior to backgrounding is capable of increasing carcass MS and improving finishing feed efficiency of beef steers, potentially through metabolic imprinting. Theories of the potential physiological mechanisms responsible for these improvements have been reported and are currently under evaluation. Although the economic relevance of such improvements may vary widely across production scenarios and market prices, the benefits associated with these production practices may be capable of enhancing finishing feed efficiency and carcass MS for beef production systems that utilize early weaning as a management practice.

**LITERATURE CITED**


Table 1. Description of $n$ and age$^1$ of steers$^2$ within each contemporary group$^3$.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Year 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>13</td>
<td>10</td>
<td>103</td>
<td>85</td>
<td>116</td>
<td>203</td>
<td>185</td>
<td>116</td>
<td>356</td>
<td>338</td>
<td>369</td>
<td>475</td>
<td>439</td>
<td>508</td>
</tr>
<tr>
<td>Fall</td>
<td>9</td>
<td>12</td>
<td>104</td>
<td>94</td>
<td>115</td>
<td>252</td>
<td>242</td>
<td>263</td>
<td>406</td>
<td>396</td>
<td>417</td>
<td>510</td>
<td>493</td>
<td>531</td>
</tr>
<tr>
<td>Year 2</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>11</td>
<td>10</td>
<td>114</td>
<td>87</td>
<td>125</td>
<td>212</td>
<td>185</td>
<td>223</td>
<td>370</td>
<td>343</td>
<td>381</td>
<td>499</td>
<td>472</td>
<td>510</td>
</tr>
<tr>
<td>Fall</td>
<td>12</td>
<td>13</td>
<td>122</td>
<td>111</td>
<td>142</td>
<td>198</td>
<td>180</td>
<td>211</td>
<td>410</td>
<td>380</td>
<td>435</td>
<td>535</td>
<td>482</td>
<td>581</td>
</tr>
</tbody>
</table>

$^1$Age is represented in d.

$^2$Steers were either early weaned (EW; received concentrated ad libitum and were limit-fed cool season grass hay at a rate of 0.68 kg per steer per d in a dry lot between early and conventional weaning) or conventionally (weaned; remained unsupplemented with dams until removal). All steers were commingled at the time of conventional weaning, backgrounded on pasture, and finished in a feedlot.

$^3$Contemporary groups were defined by year and season of birth.
Table 2. Average ingredient and nutrient composition of final concentrate provided to EW\textsuperscript{1} steers during the early dry-lot feeding phase and all steers during the finishing\textsuperscript{2} phase.

<table>
<thead>
<tr>
<th>Item, % of DM</th>
<th>Early dry-lot</th>
<th>Finishing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ingredient</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cracked corn</td>
<td>41.00</td>
<td>-</td>
</tr>
<tr>
<td>Ground corn</td>
<td>-</td>
<td>49.28</td>
</tr>
<tr>
<td>Distiller’s dried grains with solubles</td>
<td>15.00</td>
<td></td>
</tr>
<tr>
<td>Dried corn gluten feed</td>
<td>15.00</td>
<td>38.68</td>
</tr>
<tr>
<td>Wheat middlings</td>
<td>10.45</td>
<td>10.20</td>
</tr>
<tr>
<td>Cottonseed hulls</td>
<td>10.00</td>
<td>-</td>
</tr>
<tr>
<td>Liquid cane molasses</td>
<td>6.00</td>
<td>-</td>
</tr>
<tr>
<td>Limestone</td>
<td>2.00</td>
<td>1.43</td>
</tr>
<tr>
<td>Salt</td>
<td>0.50</td>
<td>0.36</td>
</tr>
<tr>
<td>Vitamin ADE premix\textsuperscript{3}</td>
<td>0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>Rumensin 90\textsuperscript{4}</td>
<td>-</td>
<td>0.02</td>
</tr>
<tr>
<td>Nutrient\textsuperscript{5}</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM\textsuperscript{6}</td>
<td>89.90</td>
<td>90.60</td>
</tr>
<tr>
<td>CP</td>
<td>16.70</td>
<td>16.70</td>
</tr>
<tr>
<td>NDF</td>
<td>28.43</td>
<td>21.94</td>
</tr>
<tr>
<td>ADF</td>
<td>14.28</td>
<td>7.80</td>
</tr>
<tr>
<td>Ether extract</td>
<td>4.48</td>
<td>3.95</td>
</tr>
<tr>
<td>NE\textsubscript{m}, Mcal per kg</td>
<td>1.79</td>
<td>1.96</td>
</tr>
<tr>
<td>NE\textsubscript{g}, Mcal per kg</td>
<td>1.19</td>
<td>1.30</td>
</tr>
</tbody>
</table>

\textsuperscript{1}Early weaned (EW) steers were weaned at an average of 111 d of age and provided \textit{ad libitum} access to concentrate and limit-fed mixed cool season grass hay at a rate of 0.68 kg per head per d for an average of 104 d in a dry-lot setting. Steers were initially offered a commercially-manufactured starter ration (Southern States Cooperative, Richmond, VA 23294) for 5 d, and were then transitioned to a final concentrate by replacing soybean meal with dried corn gluten feed and wheat middlings in a linear fashion over a series of 4 steps which occurred at 21-d intervals.

\textsuperscript{2}Commingled EW and conventionally weaned (CW) steers were finished within season of birth and year of birth-based groups in a feedlot setting for an average of 121 d following a backgrounding period that averaged 153 d.

\textsuperscript{3}Vitamin ADE premix contained 22,046,200 IU/kg Vitamin A, 8,818,480 IU/kg Vitamin D, and 22,046 IU/kg Vitamin E (Augusta Cooperative Farm Bureau, Inc., Staunton, VA 24401).

\textsuperscript{4}Type A medicated article contained 200 g per kg of Monensin USP (Elanco Animal Health, Greenfield, IN 46140).

\textsuperscript{5}Analyzed by an independent laboratory (Cumberland Valley Analytical Services, Hagerstown, MD 21742).

\textsuperscript{6}DM is expressed on an as-fed basis.
Table 3. Average component\(^1\) and nutrient composition of the final TMR\(^2\) provided to steers throughout the finishing phase.

<table>
<thead>
<tr>
<th>Item, % of DM</th>
<th>Year 1</th>
<th>Year 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Fall</td>
</tr>
<tr>
<td>Component</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corn silage</td>
<td>12.87</td>
<td>11.97</td>
</tr>
<tr>
<td>Concentrate pellet</td>
<td>87.13</td>
<td>88.03</td>
</tr>
<tr>
<td>Nutrient</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM(^3)</td>
<td>76.20</td>
<td>75.40</td>
</tr>
<tr>
<td>CP</td>
<td>14.80</td>
<td>16.40</td>
</tr>
<tr>
<td>NDF</td>
<td>30.50</td>
<td>24.70</td>
</tr>
<tr>
<td>ADF</td>
<td>17.10</td>
<td>10.30</td>
</tr>
<tr>
<td>Ether extract</td>
<td>4.80</td>
<td>4.90</td>
</tr>
<tr>
<td>NE(_m), Mcal per kg</td>
<td>1.83</td>
<td>1.81</td>
</tr>
<tr>
<td>NE(_g), Mcal per kg</td>
<td>1.21</td>
<td>1.19</td>
</tr>
</tbody>
</table>

\(^1\)Total mixed rations (TMR) offered to commingled early weaned (EW) and conventionally weaned (CW) steers throughout finishing were prepared and offered daily by blending a commercially manufactured concentrate pellet with corn silage.

\(^2\)Steers were initially adapted to corn silage during the final 7 d of the backgrounding phase, which concluded with shipment to the feedlot. Upon arrival to the feedlot, steers were adapted to a final total mixed finishing ration in a step-wise fashion by replacing corn silage with concentrate pellet in a linear fashion over an additional 21-d period that consisted of three additional steps.

\(^3\)DM is expressed on an as-fed basis.
### Table 4. Least square means of BW and ADG for treatment\(^1\), season\(^2\) and year\(^3\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Year 1</th>
<th>Year 2</th>
<th>SEM(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>EW</td>
</tr>
<tr>
<td>BW, kg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth(^5,6)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>36.7</td>
<td>38.7</td>
<td>36.1</td>
</tr>
<tr>
<td>CW</td>
<td>132.2</td>
<td>133.9</td>
<td>137.9</td>
</tr>
<tr>
<td>Early weaning(^6)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>251.4</td>
<td>210.0</td>
<td>344.3</td>
</tr>
<tr>
<td>Conventional weaning(^7,8,9)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>355.1</td>
<td>330.4</td>
<td>399.3</td>
</tr>
<tr>
<td>Backgrounding(^8,9)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>493.3(^c)</td>
<td>519.1(^bc)</td>
<td>557.0(^bc)</td>
</tr>
<tr>
<td>ADG, kg per d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth to early weaning(^10)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>0.89(^b)</td>
<td>0.93(^ab)</td>
<td>0.96(^ab)</td>
</tr>
<tr>
<td>Early to conventional weaning(^10)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>1.27(^a)</td>
<td>0.86(^b)</td>
<td>1.39(^a)</td>
</tr>
<tr>
<td>Backgrounding(^7,8,9)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>0.64</td>
<td>0.79</td>
<td>0.36</td>
</tr>
<tr>
<td>Finished(^10)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EW</td>
<td>1.31(^b)</td>
<td>1.47(^b)</td>
<td>1.54(^b)</td>
</tr>
</tbody>
</table>

\(^a,b,c\) Means within a row without a common superscript differ \((P < 0.05)\).

\(^1\) Treatments were early weaned (EW; steers averaged 111 d of age at weaning and were provided ad libitum access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d) and conventionally weaned (CW; previously unsupplemented steers remained with dams until weaning at an average of 215 d of age). All steers were commingled and backgrounded in a grazing setting for an average of 153 d prior to finishing.

\(^2\) Season represents season of birth, and included spring and fall.

\(^3\) Year represents year of birth, and included 1 and 2.

\(^4\) Pooled standard error of the least square means.

\(^5\) Main effect of season of birth \((P < 0.10)\).

\(^6\) Main effect of year of birth \((P < 0.001)\).

\(^7\) Treatment x season of birth interaction \((P < 0.01)\).

\(^8\) Treatment x year of birth interaction \((P < 0.05)\).

\(^9\) Season of birth x year of birth interaction \((P < 0.01)\).

\(^10\) Treatment x season of birth x year of birth interaction \((P < 0.05)\).
Table 5. Least square means of ultrasound-estimated body composition at various time points for treatment\(^1\) and season\(^2\).

<table>
<thead>
<tr>
<th>Item(^3)</th>
<th>Spring</th>
<th>Fall</th>
<th>(P) - value</th>
<th>SEM(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time of early weaning</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFT(^5), cm</td>
<td>0.20</td>
<td>0.25</td>
<td>0.31</td>
<td>0.02</td>
</tr>
<tr>
<td>REA, square cm</td>
<td>29.87(^b)</td>
<td>38.13(^a)</td>
<td>&lt; 0.05</td>
<td>1.54</td>
</tr>
<tr>
<td>IMF, %</td>
<td>3.38</td>
<td>3.20</td>
<td>0.41</td>
<td>0.16</td>
</tr>
<tr>
<td>Time of conventional weaning</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFT(^6), cm</td>
<td>0.43</td>
<td>0.23</td>
<td>0.16</td>
<td>0.04</td>
</tr>
<tr>
<td>REA(^6,7), square cm</td>
<td>45.03</td>
<td>37.35</td>
<td>0.56</td>
<td>1.68</td>
</tr>
<tr>
<td>IMF, %</td>
<td>2.89(^b)</td>
<td>2.96(^b)</td>
<td>&lt; 0.05</td>
<td>0.16</td>
</tr>
<tr>
<td>Completion of backgrounding</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFT(^6), cm</td>
<td>0.53</td>
<td>0.36</td>
<td>0.45</td>
<td>0.05</td>
</tr>
<tr>
<td>REA(^8), square cm</td>
<td>57.68</td>
<td>52.58</td>
<td>0.16</td>
<td>1.80</td>
</tr>
<tr>
<td>IMF, %</td>
<td>3.69(^a)</td>
<td>2.92(^b)</td>
<td>1.66(^c)</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

\(^{a,b}\)Means within a row without a common superscript differ \((P < 0.05)\).

\(^1\)Treatments were early weaned (EW; steers averaged 111 d of age at weaning and were provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d) and conventionally weaned (CW; previously unsupplemented steers remained with dams until weaning at an average of 215 d of age).

All steers were commingled and backgrounded in a grazing setting for an average of 153 d and adapted to a final finishing ration prior to the onset of the finishing feed intake measurement period.

\(^2\)Season represents season of birth, and included spring and fall.

\(^3\)SFT = 12\(^{th}\)-rib subcutaneous fat thickness, REA = ribeye area and IMF = intramuscular fat.

\(^4\)Pooled standard error of the least square means.

\(^5\)Main effect of treatment \((P < 0.10)\).

\(^6\)Main effect of treatment \((P < 0.05)\).

\(^7\)Main effect of season \((P < 0.10)\).

\(^8\)Main effect of season of birth \((P < 0.01)\).
Table 6. Least square means of carcass measurements for treatment\textsuperscript{1}, season\textsuperscript{2} and year\textsuperscript{3}.

<table>
<thead>
<tr>
<th>Item\textsuperscript{4}</th>
<th>Year 1</th>
<th>Year 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring EW</td>
<td>Fall EW</td>
</tr>
<tr>
<td>SFT\textsuperscript{6}, cm</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>HCW\textsuperscript{7}, kg</td>
<td>307.0\textsuperscript{c}</td>
<td>320.6\textsuperscript{bc}</td>
</tr>
<tr>
<td>REA\textsuperscript{7}, square cm</td>
<td>77.1\textsuperscript{b}</td>
<td>78.2\textsuperscript{ab}</td>
</tr>
<tr>
<td>DP\textsuperscript{8}, %</td>
<td>62.3</td>
<td>62.6</td>
</tr>
<tr>
<td>KPH\textsuperscript{9}, %</td>
<td>2.6</td>
<td>2.6</td>
</tr>
<tr>
<td>YG\textsuperscript{6}</td>
<td>2.8</td>
<td>2.9</td>
</tr>
<tr>
<td>MS\textsuperscript{6,10,11}, kg</td>
<td>685.5</td>
<td>687.8</td>
</tr>
</tbody>
</table>

\textsuperscript{a,b,c} Means within a row without a common superscript differ (\(P < 0.05\)).

\textsuperscript{1}Treatments were early weaned (EW; steers averaged 111 d of age at weaning and were provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d) and conventionally weaned (CW; previously unsupplemented steers remained with dams until weaning at an average age of 215 d). All steers were commingled and backgrounded in a grazing setting for an average of 153 d prior to finishing.

\textsuperscript{2}Season represents season of birth, and included spring and fall.

\textsuperscript{3}Year represents year of birth, and included 1 and 2.

\textsuperscript{4}DP = dressing percent, SFT = 12\textsuperscript{th}-rib subcutaneous fat thickness, REA = ribeye area, YG = yield grade and MS = marbling score.

\textsuperscript{5}Pooled standard error of the least square means.

\textsuperscript{6}Main effect of year of birth (\(P < 0.01\)).

\textsuperscript{7}Treatment x season of birth x year of birth interaction (\(P < 0.05\)).

\textsuperscript{8}Season of birth x year of birth interaction (\(P < 0.05\)).

\textsuperscript{9}Main effect of year of birth (\(P < 0.10\)).

\textsuperscript{10}Main effect of treatment (\(P < 0.01\)).

\textsuperscript{11}400 = slight\textsuperscript{00}, 500 = small\textsuperscript{00}, 600 = modest\textsuperscript{00}, 700 = moderate\textsuperscript{00}, 800 = slightly abundant\textsuperscript{00}.
Table 7. Least square means of BW, BW^{0.75}, ADG and calculated NE_{m} requirement during the finishing feed intake measurement period\(^1\) for treatment\(^2\) and season\(^3\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Spring</th>
<th>Fall</th>
<th>P - value</th>
<th>SEM(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>EW</td>
<td>CW</td>
</tr>
<tr>
<td>Initial BW, kg</td>
<td>371.1(^b)</td>
<td>361.1(^b)</td>
<td>433.1(^a)</td>
<td>381.5(^b)</td>
</tr>
<tr>
<td>Final BW, kg</td>
<td>510.9(^b)</td>
<td>540.0(^ab)</td>
<td>586.1(^a)</td>
<td>535.5(^b)</td>
</tr>
<tr>
<td>Total BW gain, kg</td>
<td>139.8(^b)</td>
<td>178.9(^a)</td>
<td>153.0(^ab)</td>
<td>153.9(^ab)</td>
</tr>
<tr>
<td>Average BW, kg</td>
<td>442.3(^b)</td>
<td>453.7(^b)</td>
<td>509.6(^a)</td>
<td>458.5(^b)</td>
</tr>
<tr>
<td>Average BW(^{0.75}), kg</td>
<td>79.1(^b)</td>
<td>80.6(^b)</td>
<td>88.0(^a)</td>
<td>81.3(^b)</td>
</tr>
<tr>
<td>ADG, kg per d</td>
<td>1.7</td>
<td>1.6</td>
<td>1.7</td>
<td>1.8</td>
</tr>
<tr>
<td>Calculated NE_{m} requirement, Mcal per d</td>
<td>13.0(^b)</td>
<td>13.2(^b)</td>
<td>14.5(^a)</td>
<td>13.4(^b)</td>
</tr>
</tbody>
</table>

\(^{a,b}\)Means within a row without a common superscript differ (P < 0.05).

\(^1\)Feed intake was measured daily over a duration of 67 to 118 d for steers born in the spring and 77 to 106 d for steers born in the fall.

\(^2\)Treatments were early weaned (EW; steers averaged 111 d of age at weaning and were provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d) and conventionally weaned (CW; previously unsupplemented steers remained with dams until weaning at an average age of 215 d).

All steers were commingled and backgrounded in a grazing setting for an average of 153 d and adapted to a final finishing ration prior to the onset of the finishing feed intake measurement period.

\(^3\)Season represents season of birth, and included spring and fall.

\(^4\)Pooled standard error of the least square means.
### Table 8. Least square means of finishing feed intake and efficiency during the measurement period\(^1\) for treatment\(^2\) and season\(^3\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Spring</th>
<th>Fall</th>
<th>P - value</th>
<th>SEM(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>EW</td>
<td>CW</td>
</tr>
<tr>
<td>Observed feed intake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, kg DM</td>
<td>783.6(^b)</td>
<td>1117.8(^a)</td>
<td>1053.2(^a)</td>
<td>1020.9(^a)</td>
</tr>
<tr>
<td>ADFI(^5), kg DM per d</td>
<td>9.5</td>
<td>10.0</td>
<td>11.8</td>
<td>11.9</td>
</tr>
<tr>
<td>ADFI(^5), Mcal NE(_{eq}) per d</td>
<td>11.3</td>
<td>11.9</td>
<td>14.3</td>
<td>14.4</td>
</tr>
<tr>
<td>ADFI(^5,6), NE(_{eq}) equivalents per d</td>
<td>1.3</td>
<td>1.4</td>
<td>1.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Residual NE(<em>{eq}) intake(^5,7), Mcal NE(</em>{eq}) per d</td>
<td>4.4</td>
<td>5.0</td>
<td>7.1</td>
<td>8.4</td>
</tr>
<tr>
<td>Predicted feed intake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADFI(^5), kg DM per d</td>
<td>9.8</td>
<td>9.6</td>
<td>12.0</td>
<td>11.7</td>
</tr>
<tr>
<td>ADFI(^5), Mcal NE(_{eq}) per d</td>
<td>11.6</td>
<td>11.5</td>
<td>14.5</td>
<td>14.2</td>
</tr>
<tr>
<td>Efficiency</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G:F, kg of BW gain per kg DM</td>
<td>0.17(^a)</td>
<td>0.17(^a)</td>
<td>0.15(^b)</td>
<td>0.16(^{ab})</td>
</tr>
<tr>
<td>Residual NE(_{eq}) efficiency(^5,7), Mcal per kg</td>
<td>2.61</td>
<td>3.05</td>
<td>4.16</td>
<td>4.67</td>
</tr>
<tr>
<td>BW gain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RFI(^5,8), kg DM per d</td>
<td>-0.53</td>
<td>0.51</td>
<td>-0.18</td>
<td>0.28</td>
</tr>
<tr>
<td>RFI(^5,8), Mcal NE(_{eq}) per d</td>
<td>-0.64</td>
<td>0.61</td>
<td>-0.22</td>
<td>0.34</td>
</tr>
</tbody>
</table>

\(^{a,b}\)Means within a row without a common superscript differ (P < 0.05).

\(^1\)Feed intake was measured daily over a duration of 67 to 118 d for steers born in the spring and 77 to 106 d for steers born in the fall.

\(^2\)Treatments were early weaned (EW; steers averaged 111 d of age at weaning and were provided *ad libitum* access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for an average of 104 d) and conventionally weaned (CW; previously unsupplemented steers remained with dams until weaning at an average of 215 d of age). All steers were commingled and backgrounded in a grazing setting for an average of 153 d and adapted to a final finishing ration prior to the onset of the finishing feed intake measurement period.

\(^3\)Season represents season of birth, and included spring and fall.

\(^4\)Pooled standard error of the least square means.

\(^5\)Main effect of season (P < 0.0001).

\(^6\)Main effect of treatment (P < 0.05).

\(^7\)Main effect of treatment (P < 0.10).

\(^8\)RFI = residual feed intake.
Chapter III: Alternative weaning and finishing strategies for beef steers I: Effects on growth performance, finishing feed efficiency, visceral organ mass and carcass traits

Jason K. Smith

ABSTRACT

Increased volatility in climate, grain prices and grid-based carcass premiums have led beef producers to search for alternative weaning and finishing management strategies that provide options to more conventional practices. An experiment was conducted to evaluate the effects of an alternative weaning strategy and finishing ration on growth performance, finishing feed efficiency, visceral organ mass and carcass traits. Angus (ANG) and Simmental (SIM) sired steers were randomly assigned to one of two weaning treatments [early weaned (EW; weaned at an average age of 111 d; n = 14) or conventionally weaned (CW; weaned at an average age of 233 d; n = 14)] and one of two finishing treatments [high corn (HC; 68.7 % of DM from steam-flaked corn; n = 14) or low corn (LC; 50 % of DM from steam-flaked corn isoenergetically replaced with dried corn gluten feed; n = 14)] in a 2 x 2 x 2 factorial design. Steers were commingled at the time of conventional weaning and backgrounded for 190 d before being finished for an average of 157 d and harvested in groups upon reaching an ultrasound-estimated 12th-rib subcutaneous fat thickness (SFT) of 1.0 cm. Early weaning increased ADG between the times of early and conventional weaning ($P < 0.001$), which resulted in an increase in ultrasound-estimated percent intramuscular fat (IMF) at the time of conventional weaning ($P < 0.05$) that was retained throughout backgrounding ($P < 0.01$). Although backgrounding ADG was greater for CW steers ($P < 0.05$), and ADFI was unaffected by weaning treatment ($P \geq$...
0.10), early weaning decreased finishing residual feed intake (RFI; $P < 0.01$) and lung mass ($P < 0.05$), which was inversely related to RFI ($R^2 = 0.17; P < 0.05$). Additionally, early weaning increased both dressing percent (DP; $P < 0.01$) and carcass marbling score (MS; $P < 0.01$). Replacement of corn throughout finishing increased G:F ($P < 0.05$) and decreased both lung mass ($P < 0.01$) and carcass MS ($P < 0.0001$). Collectively, these results provide additional evidence that early weaning enhances finishing feed efficiency and marbling development, while iso-caloric replacement of finishing DM from corn with dried corn gluten feed decreases finishing feed efficiency and marbling development. Furthermore, these results provide novel evidence that lung mass is related to finishing feed efficiency and is affected by source of energy at different stages of development.

INTRODUCTION

Increased volatility in feed grain prices and climate patterns have led beef cattle producers to search for alternative nutritional management strategies. As a result, producers have expressed interest in reducing their dependency upon forages during times of limited abundance, as well as reducing their dependency upon corn grain. Early weaning is one such strategy that is capable of decreasing feed resource requirements of the cow herd (Peterson et al., 1987; Llewellyn et al., 2013) while improving reproductive performance (Smith and Vincent, 1972; Laster et al., 1973; Lusby et al., 1981). Managing EW calves on a high post-weaning plane of nutrition, however, has resulted in conflicting reports of effects on finishing ADFI and feed efficiency (Myers et al., 1999b; Barker-Neef et al., 2001; Arthington et al., 2005; Scheffler et al., 2014), potentially due to the confounding effects of body size and growth potential, which was confirmed by accounting for this variation with RFI in the preceding experiment.
Researchers have also reported enhanced carcass MS of EW steers (Loy et al., 1999; Myers et al., 1999b; Meyer et al., 2005; Shike et al., 2007), with the greatest improvement reported by Scheffler et al. (2014) who included an additional pasture-based growth phase between the times of conventional weaning and finishing. Independent of weaning management strategies, the increased availability of coproducts of the corn milling industry has increased their utilization in finishing rations (Hersom et al., 2010), which often results in a reduction in NEg that corresponds with a reduction in MS (Schoonmaker et al., 2010; Luebbe et al., 2012). The mechanism responsible for this reduction, however, has yet to be determined. As such, an experiment was conducted to evaluate the effects of early weaning and isocaloric replacement of corn on marbling development, finishing RFI and visceral organ mass, as well as to identify and characterize relationships between visceral organ mass and RFI.

**MATERIALS AND METHODS**

All procedures reported herein were approved by the Virginia Tech Institutional Animal Care and Use Committee.

*Cattle and management*

Angus (n = 16) and Simmental (n = 12) sired steer progeny of the Virginia Tech commercial beef herd born in a single fall calving season were included in this experiment. Steers were sired by one of five commercial AI sires, castrated within 24 h of birth, and received initial 7-way clostridial (Vision 7; Merck and Co., Inc., White House Station, NJ 08889) and modified-live virus respiratory disease complex (Bovi Shield Gold FP5 VL5; Zoetis, Florham Park, NJ 07932) vaccinations 14 d prior to weaning. Vaccinations were repeated 14 d following
weaning, at which time all steers received a topical prophylactic doramectin (Dectomax; Zoetis, Florham Park, NJ 07932) treatment for prevention and control of internal and external parasites.

All steers were stratified by BW and sire breed before being randomly assigned to one of two weaning treatment groups [(EW; n = 14) or (CW; n = 14)] 5 d prior to early weaning. Early weaned steers were weaned at an average age of 113 d (ranged from 89 to 128 d), transported to a dry lot, and initially offered commercially-manufactured calf starter (88.90 % DM, 22.30 % CP and 1.19 Mcal of NE per kg on an as-fed basis; Southern States Cooperative, Richmond, VA 23294) ad libitum and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d. Early-weaned steers were transitioned to a custom-blended concentrate after 5 d. Concentrate formulations were adjusted at each of five proceeding 21-d intervals to decrease CP content (Table 1). Early weaned steers remained in the dry lot for a total of 124 d, throughout which time CW steers remained unsupplemented with their dams until being weaned at an average age of 231 d (ranged from 212 to 249 d).

Upon completion of the 124-d post-weaning early dry-lot feeding period for EW steers, which corresponded with the time of weaning for CW steers, EW steers were removed from the dry lot and commingled with CW steers. Commingled steers were backgrounded on warm-season annual and cool-season perennial forages in a grazing setting for 190 d. Steers were provided ad libitum access to corn silage throughout the final 21 d of the backgrounding phase, which sufficed as the initial adaptation step to the final finishing ration. Immediately following completion of the backgrounding phase, steers were transported to a covered feedlot at the Shenandoah Valley Agricultural Research and Extension Center located in Raphine, VA. Upon arrival, steers were stratified by weaning treatment, sire breed and BW before being randomly assigned to one of two finishing treatments [(HC; consisted of 69 % of DM from steam-flaked
corn) or (LC; 50 % of DM from steam-flaked corn was iso-calorically and iso-nitrogenously replaced with dried corn gluten feed)]. Relative levels of other ingredients, primarily wheat middlings, cottonseed meal, cottonseed hulls and urea, were adjusted accordingly (Table 2) in order to achieve isocaloric and isonitrogenous rations. Steers were randomly placed in one of four feedlot pens and adapted to a respective final finishing concentrate- and corn silage-based total mixed ration (TMR) in a stepwise fashion over a 42-d period (further described in Table 3). Fresh TMR was prepared daily by blending pre-mixed concentrate with corn silage immediately prior to offering, which occurred once daily between the hours of 0800 and 1000 at an initial rate of 14 kg per steer per d. Offerings were adjusted daily in 0.91-kg increments to achieve refusals of approximately 5 %. Steers were finished for an average of 157 d (ranged from 90 to 203 d), before being harvested at the Virginia Tech Meat Science Center (Blacksburg, VA 24061) in one of six groups upon reaching an ultrasound-estimated common 12\textsuperscript{th}-rib SFT of approximately 1.0 cm.

\textit{Ration composition}

Bi-weekly concentrate and hay samples of offerings to EW steers were collected throughout the early post-weaning dry-lot feeding period, and corn silage, concentrate and TMR offering samples were collected throughout the finishing phase for each finishing treatment. Samples were frozen and stored at -20 °C prior to being thawed and combined to form representative composites. Composite samples were transported to an independent laboratory (Dairy One; Ithaca, NY 14850) that used wet-chemistry methods of analysis to determine nutrient content.
Growth performance, ultrasound, and insulin and glucose

Un-shrunken BW was measured within 24 h of birth, at 21 ± 3 d intervals throughout the duration of the experiment, and at the completion of each management phase. Total and within management-phase un-shrunken BW gain was calculated by difference of measurements collected at the initiation and completion of each production phase, and used to calculate total and within management-phase ADG.

Transdermal body compositional ultrasound images were collected at the time of early and conventional weaning, completion of the backgrounding phase, at 21-d intervals throughout the first 108 d of the finishing phase, and 12 h prior to harvest in order to estimate SFT, ribeye area (REA) and percent intramuscular fat (IMF). A 36 cm x 36 cm area lateral to and projecting cranially from the ventral end of the 13th rib was clipped, brushed and coated with soybean oil to facilitate ultrasound transduction. Images were collected using an Aloka 500V real-time ultrasound machine equipped with a 17.2-cm, 3.5-MHz linear transducer (Hitachi Aloka Medical America, Inc., Wallingford, CT 06492). All images were then processed and interpreted by an independent centralized ultrasound processing laboratory (Critical Insights, Inc., Maryville, MO 64468). Additionally, images collected throughout the duration of the finishing phase were used to estimate 12th-rib SFT in real-time in order to stage harvest groups at a common ultrasound-estimated SFT-based endpoint of 1.0 cm.

Blood samples were collected via jugular venipuncture from ANG steers immediately prior to the time of early weaning, and at 21-d intervals thereafter until 108-d following feedlot arrival. Sample collection occurred between 0800 and 1000 h and was completed prior to feeding in order to provide baseline measurements of plasma insulin and serum glucose concentrations. Blood samples utilized to determine plasma insulin concentrations were
collected into 10-mL green-topped BD Vacutainers (Becton, Dickinson and Company, Franklin Lakes, NJ 07417) containing sodium heparin as an anticoagulant, and samples utilized to determine serum glucose concentrations were collected into 7-mL gray-topped BD Vacutainers containing sodium fluoride as a glycolytic inhibitor. All samples were immediately chilled on ice for a minimum of 8 h prior to centrifugation at 2,500 x g for 20 min. Serum and plasma were then decanted, frozen and stored at -20°C until further analysis. Plasma insulin concentrations were determined using a species-specific commercially-manufactured ELISA kit (Mercodia Bovine Insulin ELISA; Mercodia AB, Uppsala, Sweden) using the instructions provided by the manufacturer, and were expressed in ng per mL. Serum glucose concentrations were determined using a commercially-manufactured mutarotase-glucose oxidase enzymatic kit (Autokit Glucose; Wako Diagnostics, Mountain View, CA 94043) using the instructions for microtiter/microplate application provided by the manufacturer, and were expressed in mg per dL. The intra-assay CV for plasma insulin and serum glucose concentrations were 4.34 and 5.94 %, respectively, while the inter-assay CV were 7.04 and 6.72 %, respectively. Plasma insulin and serum glucose concentrations of samples collected following the initiation of a management phase through immediately preceding the initiation of a proceeding management phase were averaged to provide an average concentration within the respective phase.

*Finishing feed intake, feed efficiency and visceral organs*

Daily individual feed intake was measured using a Calan-Broadbent feed intake measurement system (American Calan, Inc., Northwood, NH 03261). Steers were trained to individual Calan gates, with training initiated upon arrival to the feedlot and completed at the time of transition to the final adaptation step. Initiation of the daily individual feed intake measurement period corresponded with transition to the final finishing ration, and completion
corresponded with one d preceding harvest. Finishing TMR offerings and refusals were weighed daily to the nearest 0.05 kg, and daily as-fed TMR intake was calculated by difference.

As-fed ADFI was calculated by dividing the sum of as-fed TMR intake observations by the duration of the intake data collection period expressed in d, and ADFI was then expressed in units of DM and NE\(_g\). Gross unadjusted feed efficiency (G:F) expressed in kg of DM and Mcal of NE\(_g\) was calculated as the ratio of ADG in kg to ADFI in kg of DM and Mcal of NE\(_g\), respectively. In order to predict ADFI in kg of DM and Mcal of NE\(_g\), observed individual ADFI, expressed in each respective unit, was linearly regressed against average BW\(^{0.75}\), ADG, average SFT during the feed intake measurement period, and duration (DUR) of the feed intake measurement period via the Fit Model procedure of JMP Pro v.11 (SAS Institute Inc., Cary, NC 27513) using the model \(Y_j = \beta_0 + \beta_1 BW^{0.75}_j + \beta_2 ADG_j + \beta_3 SFT_j + \beta_4 DUR_j + e_j\), where \(Y_j\) represented observed ADFI of the \(j\)th animal, \(\beta_0\) represented the regression intercept, \(\beta_1 BW^{0.75}_j\) represented the partial regression coefficient for average BW\(^{0.75}\) of the \(j\)th steer, \(\beta_2 ADG_j\) represented the partial regression coefficient for ADG of the \(j\)th steer, \(\beta_3 SFT_j\) represented the partial regression coefficient for average SFT of the \(j\)th steer, \(\beta_4 DUR_j\) represented the partial regression coefficient for DUR of the \(j\)th steer, and \(e_j\) represented the random error associated with the \(j\)th steer. Residual feed intake (RFI) was then calculated as the difference between observed and predicted ADFI expressed in kg of DM and Mcal of NE\(_g\).

Steers were eviscerated immediately following harvest, which corresponded with 1 d proceeding completion of the finishing feed intake measurement period. Visceral organs were separated via combination of blunt and surgical dissection, and were trimmed and stripped to remove any remaining mesentery, blood and digesta immediately following removal from the animal. Trimmed and stripped individual organs were then rinsed with water and allowed to
drip-dry prior to being weighed to the nearest 0.02 kg. Mass was then expressed on a g per kg of shrunk BW-basis (24-h shrunk BW was measured immediately prior to harvest) in order to prevent any bias associated with relationships between visceral organ mass and body size.

**Carcass**

Trimmed and washed HCW was measured immediately following evisceration and prior to transportation to a cooler, and used to calculate DP. Carcasses were then chilled at 2.8 °C for 24 h. The right side of each chilled carcass was ribbed between the 12th and 13th costae in order to facilitate carcass data collection. Carcasses were evaluated by three trained analysts in order to measure SFT and REA, as well as estimate KPH and MS. Measurements were then averaged across analysts and used to calculate USDA yield grade (YG).

**Statistical analyses**

All statistical analyses were conducted using JMP Pro, and steer was considered the experimental unit. Analysis of variance for a 2 x 2 x 2 factorial model was conducted via the Fit Model procedure to determine the fixed interaction and main effects of weaning treatment, finishing treatment and sire breed on all response variables. Age at the time of measurement and sire nested within sire breed were used as a covariate and blocking factor, respectively, in all initial statistical models. Feedlot pen was also included as a blocking factor for growth and feed efficiency response variables measured during the finishing phase, as well as for all carcass measurements. Un-shrunk BW was utilized as a covariate for ultrasound-estimated REA, and carcass SFT was utilized as a covariate for ultrasound-estimated IMF at harvest, HCW and carcass MS. Additionally, HCW was utilized as a covariate for carcass REA. Resulting data were initially evaluated to verify equality of variance and normality by plotting residual by predicted values for each response variable. Although negatively skewed data were observed for
carcass REA and MS, transformations were unsuccessful at achieving normality, and untransformed data were analyzed. Plots of residual by predicted values were used to visually detect potential outliers. No more than three observations within each individual response variable were identified as outliers and subsequently excluded from further analysis. Final statistical models were reduced in a step-wise fashion to remove statistically insignificant interaction effects, while the main effects of weaning treatment, finishing treatment and sire breed remained in all final models. Least square means were generated through ordered difference reports and separated using the Tukey-Kramer honestly significant difference method. All interaction and main effects were considered statistically significant at \( P < 0.05 \), considered as having a tendency toward significance at \( P \geq 0.05 \) and \( < 0.10 \), and considered statistically insignificant at \( P > 0.10 \). Additionally, carcass MS was regressed against ultrasound-estimated IMF to validate ultrasound measurements used to estimate IMF, and RFI was linearly regressed against individual and total visceral organ mass to identify and characterize relationships between visceral organ mass and RFI.

**RESULTS AND DISCUSSION**

*Ration composition*

Ingredient and nutrient composition of concentrate provided *ad libitum* to EW steers during each phase of the early post-weaning dry-lot feeding period are reported in Table 1. Concentrate CP content decreased inversely with phase advancement, as a function of design, and met or exceeded the CP requirement for growing calves reported by the NRC (1996). Additionally, the ingredient and nutrient composition of both the HC and LC final finishing TMR fed at the completion of the adaptation period and throughout the remainder of the feed
intake measurement period are reported in Table 2. Due to the minimal numeric differences that existed across finishing rations, approximately 50% of the finishing DM from steam-flaked corn in the HC ration was iso-calorically and relatively iso-nitrogenously replaced with dried corn gluten feed in the LC ration through exchanging wheat middlings for cottonseed meal, cottonseed hulls and urea.

**Growth performance, ultrasound, and glucose and insulin**

Least square means of unshrunk BW and ADG, ultrasound measurements, and insulin and glucose concentrations are reported in Tables 4, 5 and 6, respectively. No three- or two-way interactions between weaning treatment, finishing treatment and sire breed were observed ($P \geq 0.13$). As expected due to stratification prior to the assignment of treatments, BW, ultrasound-estimated SFT, REA and IMF, as well as serum glucose and plasma insulin concentrations measured at or prior to the time of early weaning did not differ between weaning treatments ($P \geq 0.38$), finishing treatments ($P \geq 0.61$), or sire breeds ($P \geq 0.10$). As a result of the high plane of nutrition incurred by EW steers during the early dry-lot feeding period, ADG between the times of early and conventional weaning was approximately 1.75-fold greater ($P < 0.0001$) for EW than CW steers, which resulted in a 61-kg advantage in BW ($P < 0.0001$) at the time of conventional weaning. This elevated level of growth also resulted in 2.7- ($P < 0.0001$), 1.13- ($P < 0.01$) and 1.34-fold ($P < 0.05$) elevations in ultrasound-estimated SFT, REA and IMF, respectively, for EW steers upon completion of the early dry-lot feeding period. Nayananjalie et al. (2015a) observed increased phosphorylation ratios of ribosomal protein S6 and S6 kinase 1, two signaling proteins involved in muscle hypertrophy, for EW steers during this management phase. Activated in response to insulin (Bolster et al., 2002), these proteins are key components of the mammalian target of rapamycin (mTOR) signal transduction pathway associated with
muscle protein synthesis, and independently explained 25 and 22% of the variation in ADG (Nayananjalie et al., 2015a). In the present experiment, average plasma insulin concentration between the times of early and conventional weaning was more than 3-fold greater for EW than CW steers ($P < 0.01$). Due to the elevated plane of nutrition incurred by EW steers during this period, and the presumed increase in energy substrates that would ensue, EW steers required a greater amount of insulin to maintain a similar serum glucose concentration ($P = 0.83$) to their CW contemporaries. Based upon this, it is likely that increased phosphorylation of proteins involved in muscle hypertrophy in response to insulin was responsible for the elevated REA of EW steers at the time of conventional weaning in the present experiment. Although Schoonmaker et al. (2004) reported no effect of providing EW calves with ad libitum access to concentrate in a dry lot on ultrasound-estimated IMF when compared to CW contemporaries that remained unsupplemented with their dams, cattle utilized in their experiment received a growth implant at approximately 150 d of age. Due to the inhibitory effect of anabolic growth implants on marbling development during early periods of growth (Bruns et al., 2005), it is possible that implanting calves during the EW dry-lot feeding period resulted in the lack of an effect observed by these authors. It is likely that the elevated baseline plasma insulin concentration observed for EW steers during the early dry-lot feeding period upregulated expression of $PPAR_\gamma$, the major regulator of adipogenesis (Rosen and MacDougald, 2006), which has been shown to increase soon after the time of early weaning (Moisá et al., 2014). When combined with the expected increase in energy substrate supply associated with the high post-weaning plane of nutrition incurred by EW steers, insulin-induced upregulation of the $PPAR_\gamma$ regulatory network likely enhanced marbling development and led to the observed increase in IMF observed in the present...
experiment. No other reports could be found that compared ultrasound-estimated IMF of EW to CW steers at the time of conventional weaning.

The advantage in BW of EW steers, however, was lost throughout the backgrounding phase, as CW steers experienced a 12% increase in ADG over their EW contemporaries \( (P < 0.05) \), which resulted in the arrival of EW and CW steers to the feedlot at a similar BW \( (P = 0.20) \). This increase in ADG of CW steers was likely the result of compensatory growth resulting from a previously insufficient plane of nutrition, as numerous authors have observed that CW calves later compensate for a limited rate of growth incurred between the times of early and conventional weaning (Green and Buric, 1953; Harvey et al., 1975; Story et al., 2000; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Scheffler et al., 2014; Nayananjalie et al., 2015a; Nayananjalie et al., 2015b). Independent of the effects attributed to weaning treatment, ANG steers had a greater ultrasound-estimated SFT than SIM steers at the time of conventional weaning \( (P < 0.01) \), but no other time points \( (P \geq 0.69) \). Although IMF development was minimal during the backgrounding phase, EW steers maintained their advantage and arrived at the feedlot with an elevated level of IMF \( (P < 0.01) \) that was similar in magnitude to the difference observed upon completion of the early dry-lot feeding period, indicating retention of IMF throughout backgrounding. Additionally, EW steers maintained a portion of their advantage in REA throughout the backgrounding phase and arrived at the feedlot with a larger REA \( (P < 0.05) \) but similar SFT \( (P = 0.79) \) to their CW contemporaries, indicating that CW steers accumulated while EW steers lost subcutaneous fat throughout the backgrounding phase.

Although numerically, but not significantly greater at all previous time points \( (P \geq 0.10) \), SIM-sired steers tended to be approximately 27 kg heavier upon arrival to the feedlot \( (P = 0.07) \).
due to a 29 % increase in ADG throughout backgrounding ($P < 0.05$). Finishing ADG was also 10 % greater for SIM than ANG steers ($P < 0.01$), however no effects of sire breed were observed for REA or IMF at any time points ($P \geq 0.22$).

As a result of stratification prior to treatment assignment, BW and ADG measurements preceding feedlot arrival did not differ across finishing treatments ($P \geq 0.13$). Furthermore, finishing steers to a common ultrasound-estimated SFT resulted in all steers, regardless of weaning treatment, finishing treatment or sire breed, being harvested at a similar BW ($P \geq 0.15$). Although not different at any other time points ($P \geq 0.55$), replacement of 50 % of the steam-flaked corn with dried corn gluten feed in the final finishing ration resulted in a 30 % reduction in ultrasound-estimated IMF ($P < 0.01$) when measured at the time of harvest, indicating that isocaloric replacement of steam-flaked corn with dried corn gluten feed inhibited marbling development.

Conflicting results exist over the preference of intramuscular adipocytes for glucose or acetate as a precursor for fatty acid synthesis, as Smith and Crouse (1984) suggested an in vitro preference for glucose over acetate, while Miller et al. (1991) suggested a preference for acetate over glucose. More recently, however, Nayananjalie et al. (2015b) reported similar in vivo fractional palmitate synthesis rates from acetate and glucose in intramuscular adipose, which suggested that marbling development is dependent upon energy density, rather than form. When combined with the reduction in ultrasound-estimated IMF that resulted from isocaloric replacement of steam-flaked corn with dried corn gluten feed, the lack of a substrate preference for intramuscular adipogenesis reported by Nayananjalie et al. (2015b) provides additional evidence that marbling development is indeed dependent upon energy availability that exceeds the capacity for utilization for lean tissue growth. Although isocaloric replacement of steam-
flaked corn with dried corn gluten feed was achieved in the present experiment, such replacement likely resulted in a finishing ration that was inherently lower in digestibility and overall availability of energy substrates for adipogenesis, thus affecting the propensity for marbling development. Percent IMF at the time of harvest that did not differ significantly between EW and CW steers \( (P = 0.24) \), potentially due in part by the moderate degree of variation in MS that is typically unexplained via ultrasound measurements. In the present experiment, pre-harvest ultrasound measurements explained approximately 74% of the variation in carcass MS \( (P < 0.0001) \).

**Finishing feed intake, feed efficiency and visceral organ mass**

Least square means of finishing feed intake and efficiency, as well as individual and total visceral organ mass for weaning treatment, finishing treatment and sire breed are reported in Tables 7 and 8, respectively, and linear relationships between visceral organ mass and RFI are reported in Table 9. Although no interactions were observed \( (P \geq 0.33) \), days on feed (DOF; total duration of the finishing phase) was affected by weaning treatment \( (P < 0.01) \) and finishing treatment \( (P < 0.05) \), but not sire breed \( (P = 0.55) \). On average, EW steers required 27 fewer DOF to achieve the target ultrasound-estimated SFT of 1.0 cm \( (P < 0.01) \), while replacement of 50% of the DM from steam-flaked corn with dried corn gluten feed in the final finishing ration increased DOF by 25 d \( (P < 0.05) \).

Although no interaction or main effects of weaning treatment, finishing treatment or sire breed existed for observed or predicted ADFI when expressed in either kg of DM per d or Mcal of NE\(_g\) per d \( (P \geq 0.10) \), replacement of 50% of the finishing DM from steam-flaked corn with dried corn gluten feed resulted in a 13% reduction in G:F when expressed either in kg of DM \( (P < 0.05) \) or Mcal of NE\(_g\) \( (P < 0.05) \). Replacement of corn with wet or dried corn gluten feed
typically decreases NE\textsubscript{g} and results in a corresponding reduction in G:F (Kampman and Loerch, 1989; Ham et al., 1995). This effect, however, was partially attenuated by increasing NE\textsubscript{g} through the addition of steep liquor (Macken et al., 2004), which suggested that the previously observed reduction in feed efficiency was a function of energy dilution, rather than feedstuff composition. Kampman and Loerch (1989) reported that increasing replacement of high-moisture corn with dried corn gluten feed in finishing rations results in a linear reduction in overall DM digestibility. When combined with the results observed in the present experiment, these findings indicate that the reduction in feed efficiency is more likely the result of negative associative effects on digestibility and utilization that were not accounted for by calculated NE\textsubscript{g} values.

Although various authors observed a 4 to 10 % increase in finishing G:F of EW calves when compared to their CW contemporaries (Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004), it is possible that variation attributed to BW and growth potential in the present experiment resulted in the lack of a difference in G:F between EW and CW steers \((P = 0.51)\), as these traits have historically been thought to confound ratio-based measurements of feed efficiency (Koch et al., 1963). In order to account for the variation attributed to these (and other) traits, linear regression models fitted to predict ADFI expressed in kg of DM per d and Mcal of NE\textsubscript{g} per d included regression intercepts of 0.82 and 0.59, and partial regression coefficients of 0.19 and 0.09 for average BW\textsuperscript{0.75}, 3.73 and 2.10 for ADG, -0.04 and 0.16 for average SFT and -0.02 and -0.01 for DUR, respectively. These models were capable of explaining a significant and substantial portion of the variation in observed ADFI when expressed in kg of DM per d \((P < 0.0001; R^2 = 0.72)\) and Mcal of NE\textsubscript{g} per d \((P < 0.0001; R^2 = 0.76)\), and indicate that expressing ADFI on a NE\textsubscript{g} basis is a favorable alternative to
expressing ADFI on a DM basis when calculating RFI for growth-based feed efficiency evaluations, due to the additional explanatory capability of the model. Although no other interaction effects were observed ($P \geq 0.80$), a finishing treatment x sire breed interaction existed for RFI when expressed in either kg of DM per d ($P < 0.05$) or Mcal of NE$_g$ per d ($P < 0.05$). When expressed in kg of DM per d, RFI of HC ANG steers was lower than LC ANG steers (-1.52 vs. 1.32; SEM = 0.51; $P < 0.05$), which did not differ from HC SIM (-0.16; $P \geq 0.40$) or LC SIM (0.49; $P \geq 0.18$) steers. However when expressed in Mcal of NE$_g$ per d, RFI of HC ANG steers was not only lower than LC ANG steers (-0.69 vs. 0.56; SEM = 0.37; $P < 0.01$), but was also lower than LC SIM (-0.69 vs. 0.19; SEM = 0.37; $P < 0.01$) and HC SIM steers (-0.69 vs. 0.01; SEM = 0.37; $P < 0.05$), which did not differ from one another ($P \geq 0.14$). No other reports could be found that have evaluated the effects of corn replacement in finishing rations on RFI, indicating the need for future research to determine if the interaction between finishing treatment and sire breed observed in the present experiment were the result of variation that could be attributed to a relatively small sample population, or if different biological types of cattle inherently differ in their ability to efficiently utilize different sources of energy for growth. Independent of this interaction, early weaning resulted in approximately a 1-kg of DM per d ($P < 0.05$) and approximately a 0.5-Mcal of NE$_g$ per d ($P < 0.01$) reduction in RFI, which corresponds with a 4 % improvement in finishing feed efficiency when expressed relative to observed ADFI of CW steers. These results are consistent with those of experiment 1, where early weaning resulted in a 1.25-Mcal of NE$_g$ per d reduction in RFI that corresponded with a 7 % improvement in finishing feed efficiency.

Although no three- or two-way interactions between weaning treatment, finishing treatment and sire breed were observed for total or individual visceral organ mass ($P \geq 0.10$),
early weaning resulted in a 0.52 g per kg of BW increase in lung mass \((P < 0.05)\) at the time of harvest, which was inversely related to and independently explained 17% of the variation in RFI \((P < 0.05)\). Based upon this relationship, a 1-g per kg of BW increase in lung mass would correspond with a 0.52-Mcal of NE\(_g\) reduction in RFI. Additionally, replacement of steam-flaked corn with dried corn gluten feed in the finishing ration resulted in a 0.66 g per kg of BW reduction in lung mass \((P < 0.01)\). Although little is currently known about the role of the lungs in feed efficiency, Kolath et al. (2006) reported an inverse relationship between mitochondrial respiration and RFI. This can further be interpreted to suggest a relationship between oxygen demand for mitochondrial function and feed efficiency. Although not measured in the present experiment, gaseous exchange could potentially be a limiting factor in mitochondrial function. If lung mass affects capacity for oxygen exchange, an increase in the availability of oxygen could potentially drive mitochondrial function, thus increasing the generation of energy and promoting feed efficiency. Results of the present experiment suggest that both type and amount of energy affect lung development at different stages of growth, and increased lung mass may have been responsible for a portion of the effect on RFI that was attributed to weaning and finishing treatments.

Although unaffected by weaning treatment \((P \geq 0.16)\) or sire breed \((P \geq 0.53)\), replacement of 50% of the steam-flaked corn in the finishing ration with dried corn gluten feed increased the mass of the large intestine \((P < 0.001)\) by 1.91 g per kg of BW, which was predominantly due to enlargement of the colon and rectum \((P = 0.05)\) rather than the cecum \((P = 0.52)\). Additionally, steam-flaked corn replacement resulted in a tendency toward a 0.23-g per kg of BW increased mass of the duodenum \((P = 0.09)\), but not combined small intestine \((P = 0.44)\). Independently, mass of the colon and rectum, as well as the duodenum were conversely
related to and explained 21 ($P < 0.05$) and 17 ($P < 0.05$) % of the variation in RFI, respectively. Based upon these relationships, a 1-g per kg of BW increase in mass of the colon and rectum, and duodenum, would correspond with 0.28 and 1.17 Mcal of NEg per d elevations in RFI, respectively, and suggests that replacement of steam-flaked corn in the finishing ration likely reduced ruminal degradation and/or passage rate, which likely led to an increase in the mass of the hindgut. This theory is further supported by the reduction in G:F that was observed in steers assigned to the LC finishing treatment.

Previous authors have reported that classifying cattle as low vs. high RFI corresponded with 8 to 12 % reductions in the mass of the liver (Basarab et al., 2003), kidneys (Bonilha et al., 2013) and reticulorumen (Fitzsimons et al., 2014). The latter of these authors reported that reticuloruminal mass accounted for 4 % of the variation in observed feed intake of Simmental-sired bulls, and that RFI increased by 1 kg for each 1-kg increase in mass of the reticulorumen. Although unaffected by weaning treatment, finishing treatment or sire breed ($P \geq 0.50$) in the present experiment, RFI was also conversely related to the mass of the kidneys and bladder ($R^2 = 0.22; P < 0.05$), and tended to be conversely related to the mass of the rumen ($R^2 = 0.13; P < 0.05$). The relationships reported herein are consistent with the effects reported by Bonilha et al. (2013) for the kidneys and Fitzsimons et al. (2014) for the reticulorumen. Nonetheless, it appears that the role that the mass of individual organs play in efficiency may vary across cattle populations, and is impacted by plane of nutrition at various stages of growth. Additionally, the combined mass of all visceral organs was conversely related to RFI in the present experiment ($R^2 = 0.17; P < 0.05$), indicating that RFI increased linearly with overall visceral organ mass. Observed feed intake has been reported to be conversely associated with the mass of metabolically active visceral organs, which is conversely related to fasting heat production.
(Koong et al., 1985). These authors went on to describe that NE\textsubscript{m} is that required to maintain energy equilibrium, which is equal to fasting heat production. The concept of NE\textsubscript{m} has been adopted by the National Research Council, and is more simply stated as the fasting heat production at which BW is maintained without growth. Based upon the converse relationships between visceral organ mass and RFI reported herein, and that between RFI and the ME requirement for maintenance reported by Castro Bulle et al. (2007), it is likely that visceral organ mass and the associated fasting heat production is partially responsible for a reduction in NE\textsubscript{m} requirements of cattle with relatively low RFI.

**Carcass measurements**

Least square means of weaning treatment, finishing treatment and sire breed for carcass measurements are reported in Table 10. No weaning treatment x finishing treatment x sire breed, weaning treatment x finishing treatment or weaning treatment x sire breed interactions were observed for any carcass measurements ($P \geq 0.37$). Although LC SIM steers were harvested at what tended to be a lesser SFT than HC SIM steers (0.81 vs. 1.12 cm; SEM = 0.12; $P = 0.05$), which did not differ from HC ANG (0.98 cm; $P \geq 0.63$) or LC ANG (1.02 cm; $P \geq 0.67$) steers, EW and CW steers were harvested at a similar ($P = 0.68$) SFT-based endpoint. As expected, due to the numeric but not statistically significant differences that were observed for final BW and the inherent differences that exist in mature BW between breeds of Continental and European influence, SIM steers had approximately a 24-kg greater HCW than ANG steers ($P < 0.01$). Nonetheless, HCW was unaffected by weaning ($P = 0.66$) and finishing ($P = 0.88$) treatments. Additionally, DP was approximately 1.4 % greater for EW than CW steers ($P < 0.01$), and 1.6 % greater for ANG- than SIM-sired steers ($P < 0.05$), but was unaffected by finishing treatment.
Gut fill could potentially explain a portion of the differences observed in DP, as reductions in RFI would likely correspond with reductions in gut fill.

Although weaning treatment, finishing treatment and sire breed had no effect on REA ($P \geq 0.18$), KPH ($P \geq 0.24$) or YG ($P \geq 0.19$), early weaning resulted in a 9 % elevation in carcass MS ($P < 0.01$) when cattle were harvested at a common SFT-based endpoint. Conflicting observations have been reported by other authors who finished cattle immediately following weaning, with some reporting no effect of early weaning on MS (Myers et al., 1999c; Barker-Neef et al., 2001; Schoonmaker et al., 2001; Schoonmaker et al., 2004; Arthington et al., 2005; Moriel et al., 2014a), and others reporting advantages of EW cattle that ranged from 4 to 10 % (Loy et al., 1999; Myers et al., 1999a; Meyer et al., 2005; Shike et al., 2007). Additionally, Scheffler et al. (2014), who managed cattle similarly to the practices utilized herein, reported a similar effect as the current observation, albeit to a greater magnitude.

While unaffected by sire breed ($P = 0.91$), replacement of 50 % of the finishing DM from steam-flaked corn with dried corn gluten feed resulted in a 20 % reduction in carcass MS ($P < 0.0001$). Although there have been multiple reports that replacement of 30 to 50 % of the dietary DM from corn with coproducts of the corn-milling industry has little to no effect on MS of finished cattle (Al-Suwaiegh et al., 2002; Corrigan et al., 2009), more recent results reported by Schoonmaker et al. (2010) indicated an inverse relationship between increasing coproduct inclusion (as a replacement for dry-rolled corn and soybean meal) and carcass MS for cattle finished with concentrate-based rations. Additionally, results reported by Luebbe et al. (2012) indicated a linear reduction in MS associated with replacement of finishing DM from dry-rolled corn with such coproducts. Upon accounting for differences in DMI and ration NE$_g$ in the latter of these experiments, the treatment that replaced almost half of the DM from corn with
coproducts resulted in an average total daily NE\textsubscript{g} intake that differed by 9 % from that of the control group. Interestingly, cattle assigned to the same treatment group also displayed a 9 % reduction in carcass MS when compared to cattle that received rations that replaced no corn with WDGS, suggesting that the reduction in marbling development observed by Luebbe et al. (2012) may have been a function of energy dilution resulting from the inclusion of a low-starch feedstuff. Although a substantial reduction in MS was observed after replacing steam-flaked corn with dried corn gluten feed in the present experiment, it is possible that the reduction in marbling development was a function of a lower digestibility of the LC finishing ration, rather than a preference of IMF for energy substrates derived from a corn-based ration, as previously mentioned. This theory, however, remains to be evaluated experimentally.

**CONCLUSIONS AND IMPLICATIONS**

Results reported herein suggest that early weaning, when proceeded by a short *ad libitum* concentrate feeding period prior to backgrounding increases IMF development between the times of early and conventional weaning. This elevation in IMF is retained throughout the backgrounding phase and remains evident as marbling in the finished carcass. Additionally, this management strategy increased lung mass when measured immediately following harvest, and finishing feed efficiency when measured in the form of RFI. Although the value of these improvements inherently varies across different economic scenarios, the EW management strategies reported herein may be utilized by producers to improve finishing feed efficiency and marbling development, or by producers that routinely utilize early weaning as a reproductive or drought mitigation strategy.
Additionally, these results provide evidence of an inverse linear relationship between lung mass and RFI, and help to explain the decrease in RFI observed for EW steers. Furthermore, 50% replacement of steam-flaked corn with dried corn gluten feed inhibited finishing IMF development and reduced carcass MS, while also negatively impacting G:F. Nonetheless, decisions related to the replacement of corn grain in finishing rations with coproducts should be based upon economics, as their impact to fed cattle profitability will be dependent upon relative availability and price of feedstuffs, as well as fed-cattle marketing strategies and quality grade-based grid marketing premiums.

LITERATURE CITED


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Table 1. Average ingredient and nutrient composition\(^1\) of concentrate and hay provided to EW\(^2\) steers during the post-weaning early dry-lot feeding period.

<table>
<thead>
<tr>
<th>Item(^4), % of DM</th>
<th>Phase(^3)</th>
<th>Hay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Ingredient</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cracked corn</td>
<td>34.63</td>
<td>39.81</td>
</tr>
<tr>
<td>DDGS</td>
<td>14.70</td>
<td>14.73</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>14.18</td>
<td>9.81</td>
</tr>
<tr>
<td>Wheat middlings</td>
<td>9.84</td>
<td>10.36</td>
</tr>
<tr>
<td>DCGF</td>
<td>9.95</td>
<td>9.20</td>
</tr>
<tr>
<td>Cottonseed hulls</td>
<td>7.95</td>
<td>8.22</td>
</tr>
<tr>
<td>Liquid molasses</td>
<td>6.19</td>
<td>5.31</td>
</tr>
<tr>
<td>Limestone</td>
<td>1.99</td>
<td>1.99</td>
</tr>
<tr>
<td>Salt</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td>Vitamin A premix(^5)</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>Nutrient</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM, % as-fed</td>
<td>88.16</td>
<td>88.03</td>
</tr>
<tr>
<td>CP</td>
<td>20.25</td>
<td>18.35</td>
</tr>
<tr>
<td>NDF</td>
<td>25.41</td>
<td>25.58</td>
</tr>
<tr>
<td>ADF</td>
<td>12.95</td>
<td>12.97</td>
</tr>
<tr>
<td>Ether extract</td>
<td>4.15</td>
<td>4.29</td>
</tr>
<tr>
<td>NE(_{\text{m}}), Mcal per kg</td>
<td>1.98</td>
<td>1.99</td>
</tr>
<tr>
<td>NE(_{\text{g}}), Mcal per kg</td>
<td>1.33</td>
<td>1.34</td>
</tr>
</tbody>
</table>

\(^1\) Analyzed by an independent laboratory (Dairy One, Ithaca, NY 14850).
\(^2\) EW = early weaned; EW steers were weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d.
\(^3\) Concentrate formulations were adjusted at each of 5 21-d intervals to decrease CP content.
\(^4\) DDGS = distiller’s dried grains with solubles; DCGF = dried corn gluten feed.
\(^5\) Contained 30,000,000 IU per kg of Vitamin A.
Table 2. Average ingredient and nutrient composition\(^1\) of the final ration provided to steers during the finishing\(^2\) phase.

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>HC</th>
<th>LC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Steam-flaked corn</td>
<td>68.65</td>
<td>33.89</td>
</tr>
<tr>
<td>Dried corn gluten feed</td>
<td>--</td>
<td>35.47</td>
</tr>
<tr>
<td>Wheat middlings</td>
<td>--</td>
<td>17.42</td>
</tr>
<tr>
<td>Cottonseed meal</td>
<td>11.10</td>
<td>--</td>
</tr>
<tr>
<td>Corn silage</td>
<td>10.59</td>
<td>10.45</td>
</tr>
<tr>
<td>Cottonseed hulls</td>
<td>5.71</td>
<td>--</td>
</tr>
<tr>
<td>Dicalcium phosphate</td>
<td>1.29</td>
<td>--</td>
</tr>
<tr>
<td>Limestone</td>
<td>1.28</td>
<td>2.5</td>
</tr>
<tr>
<td>Urea</td>
<td>1.00</td>
<td>--</td>
</tr>
<tr>
<td>Salt</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td>Trace mineral premix(^4)</td>
<td>0.09</td>
<td>0.03</td>
</tr>
<tr>
<td>Vitamin E premix(^5)</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>Selenium yeast(^6)</td>
<td>0.03</td>
<td>--</td>
</tr>
<tr>
<td>Monensin(^7)</td>
<td>0.02</td>
<td>0.02</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>HC</th>
<th>LC</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM, % as-fed</td>
<td>71.60</td>
<td>73.55</td>
</tr>
<tr>
<td>CP</td>
<td>14.40</td>
<td>13.95</td>
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<tr>
<td>NDF</td>
<td>18.90</td>
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</tr>
<tr>
<td>ADF</td>
<td>10.60</td>
<td>10.30</td>
</tr>
<tr>
<td>Ether extract</td>
<td>3.70</td>
<td>3.90</td>
</tr>
<tr>
<td>NE(_m), Mcal per kg</td>
<td>1.79</td>
<td>1.76</td>
</tr>
<tr>
<td>NE(_g), Mcal per kg</td>
<td>1.17</td>
<td>1.15</td>
</tr>
</tbody>
</table>

\(^1\)Analyzed by an independent laboratory (Dairy One, Ithaca, NY 14850).
\(^2\)Commingled early (EW) and conventionally weaned (CW) steers were finished in a covered feedlot for an average of 157 d following a 190-d backgrounding period.
\(^3\)HC = high corn; LC = low corn.
\(^4\)Contained 5.15 % Zn, 2.86 % Mn, 1.80 % Cu and 0.18 % Co (Availa-4; Zinpro Corporation, Eden Prairie, MN 55344).
\(^5\)Contained 275,578 IU per kg of Vitamin E.
\(^6\)Contained 600 ppm Se (Sel-Plex 600; Alltech Inc., Nicholasville, KY 40356).
\(^7\)Type A medicated article; contained 200 g per kg of Monensin USP (Rumensin 90; Elanco Animal Health, Greenfield, IN 46140).
Table 3. Step-wise finishing ration adaptation regimen for finishing treatments\(^1\).

<table>
<thead>
<tr>
<th>Step(^2)</th>
<th>Corn silage</th>
<th>LC concentrate</th>
<th>HC concentrate</th>
<th>Corn silage</th>
<th>LC concentrate</th>
<th>HC concentrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial(^3)</td>
<td>100</td>
<td>--</td>
<td>--</td>
<td>100</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Second</td>
<td>70</td>
<td>30</td>
<td>--</td>
<td>70</td>
<td>30</td>
<td>--</td>
</tr>
<tr>
<td>Third</td>
<td>50</td>
<td>50</td>
<td>--</td>
<td>50</td>
<td>50</td>
<td>--</td>
</tr>
<tr>
<td>Fourth</td>
<td>23</td>
<td>77</td>
<td>--</td>
<td>23</td>
<td>77</td>
<td>--</td>
</tr>
<tr>
<td>Fifth</td>
<td>23</td>
<td>52</td>
<td>25</td>
<td>23</td>
<td>77</td>
<td>--</td>
</tr>
<tr>
<td>Sixth</td>
<td>23</td>
<td>25</td>
<td>52</td>
<td>23</td>
<td>77</td>
<td>--</td>
</tr>
<tr>
<td>Final</td>
<td>23</td>
<td>--</td>
<td>77</td>
<td>23</td>
<td>77</td>
<td>--</td>
</tr>
</tbody>
</table>

\(^1\)Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^2\)Expressed on a % as-fed basis.

\(^3\)Completed prior to feedlot arrival during the conclusion of the pasture-backgrounding phase.
Table 4. Least square means\(^1\) of un-shrunk BW and ADG for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>Un-shrunk BW, kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth</td>
<td>35.67</td>
<td>36.07</td>
<td>35.09</td>
<td>36.65</td>
</tr>
<tr>
<td>Early weaning</td>
<td>149.68</td>
<td>155.82</td>
<td>155.24</td>
<td>150.26</td>
</tr>
<tr>
<td>Conventional weaning</td>
<td>308.06(^a)</td>
<td>247.03(^b)</td>
<td>279.75</td>
<td>275.34</td>
</tr>
<tr>
<td>Feedlot arrival</td>
<td>407.09</td>
<td>390.45</td>
<td>394.10</td>
<td>403.45</td>
</tr>
<tr>
<td>Harvest</td>
<td>600.20</td>
<td>605.38</td>
<td>598.04</td>
<td>607.54</td>
</tr>
<tr>
<td>ADG, kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth to early weaning</td>
<td>1.06</td>
<td>1.07</td>
<td>1.07</td>
<td>1.06</td>
</tr>
<tr>
<td>Early to conventional weaning</td>
<td>1.30(^a)</td>
<td>0.74(^b)</td>
<td>1.03</td>
<td>1.01</td>
</tr>
<tr>
<td>Backgrounding</td>
<td>1.29(^f)</td>
<td>1.45(^e)</td>
<td>1.42</td>
<td>1.31</td>
</tr>
<tr>
<td>Finishing</td>
<td>1.28</td>
<td>1.32</td>
<td>1.29</td>
<td>1.31</td>
</tr>
</tbody>
</table>

\(^{a,b}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.001)\).

\(^{c,d}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.01)\).

\(^{e,f}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.05)\).

\(^1\)No three- or two-way interactions between weaning treatment, finishing treatment or sire breed were observed \((P \geq 0.16)\).

\(^2\)Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.

\(^3\)Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^4\)Sire breeds were Angus (ANG) and Simmental (SIM).

\(^5\)Pooled standard error of the least square means.
Table 5. Least square means\(^1\) of ultrasound measurements for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item(^5)</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
</tr>
<tr>
<td>SFT, cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early weaning</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
</tr>
<tr>
<td>Conventional weaning</td>
<td>0.54(^a)</td>
<td>0.20(^b)</td>
<td>0.38</td>
</tr>
<tr>
<td>Feedlot arrival</td>
<td>0.48</td>
<td>0.38</td>
<td>0.43</td>
</tr>
<tr>
<td>Harvest</td>
<td>1.15</td>
<td>1.04</td>
<td>1.05</td>
</tr>
<tr>
<td>REA, square cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early weaning</td>
<td>38.03</td>
<td>37.88</td>
<td>36.67</td>
</tr>
<tr>
<td>Conventional weaning</td>
<td>56.29(^e)</td>
<td>49.77(^f)</td>
<td>52.01</td>
</tr>
<tr>
<td>Feedlot arrival</td>
<td>60.62(^g)</td>
<td>57.52(^h)</td>
<td>58.77</td>
</tr>
<tr>
<td>Harvest</td>
<td>83.26</td>
<td>81.04</td>
<td>80.25</td>
</tr>
<tr>
<td>IMF, %</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early weaning</td>
<td>2.34</td>
<td>2.24</td>
<td>2.36</td>
</tr>
<tr>
<td>Conventional weaning</td>
<td>3.16(^g)</td>
<td>2.35(^b)</td>
<td>2.95</td>
</tr>
<tr>
<td>Feedlot arrival</td>
<td>3.03(^e)</td>
<td>2.29(^f)</td>
<td>2.71</td>
</tr>
<tr>
<td>Harvest</td>
<td>5.59</td>
<td>5.17</td>
<td>6.34(^e)</td>
</tr>
</tbody>
</table>

\(^a,b\) Means within a factor comparison without a common superscript differ significantly \((P < 0.0001)\).
\(^c,d\) Means within a factor comparison without a common superscript differ significantly \((P < 0.001)\).
\(^e,f\) Means within a factor comparison without a common superscript differ significantly \((P < 0.01)\).
\(^g,h\) Means within a factor comparison without a common superscript differ significantly \((P < 0.05)\).

\(^1\) No three- or two-way interactions of weaning treatment, finishing treatment or sire breed were observed \((P \geq 0.13)\).
\(^2\) Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.
\(^3\) Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).
\(^4\) Sire breeds were Angus (ANG) and Simmental (SIM).
\(^5\) SFT = 12\(^{th}\)-rib subcutaneous fat thickness; REA = ribeye area; IMF = intramuscular fat.
\(^6\) Pooled standard error of the least square means.
**Table 6.** Least square means\(^1\) of plasma insulin and serum glucose concentrations for weaning treatment\(^2\) and finishing treatment\(^4\) of Angus-sired steers.

<table>
<thead>
<tr>
<th>Item</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>SEM(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
</tr>
<tr>
<td>Plasma insulin, ng/mL</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prior to early weaning</td>
<td>0.18</td>
<td>0.16</td>
<td>0.12</td>
</tr>
<tr>
<td>Early to conventional weaning</td>
<td>0.74(^c)</td>
<td>0.23(^d)</td>
<td>0.46</td>
</tr>
<tr>
<td>Backgrounding</td>
<td>0.36</td>
<td>0.34</td>
<td>0.39</td>
</tr>
<tr>
<td>Finishing</td>
<td>2.51</td>
<td>2.52</td>
<td>2.56</td>
</tr>
<tr>
<td>Serum glucose, mg/dL</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prior to early weaning</td>
<td>38.94</td>
<td>39.40</td>
<td>40.44</td>
</tr>
<tr>
<td>Early to conventional weaning</td>
<td>36.10</td>
<td>36.41</td>
<td>35.55</td>
</tr>
<tr>
<td>Backgrounding</td>
<td>37.56</td>
<td>38.36</td>
<td>37.88</td>
</tr>
<tr>
<td>Finishing</td>
<td>38.31</td>
<td>40.06</td>
<td>39.11</td>
</tr>
</tbody>
</table>

\(^a,b\) Means within a factor comparison without a common superscript differ significantly \((P < 0.0001)\).

\(^c,d\) Means within a factor comparison without a common superscript differ significantly \((P < 0.01)\).

\(^1\) No interactions between weaning treatment and finishing treatment were observed \((P \geq 0.14)\).

\(^2\) Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided *ad libitum* access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.

\(^3\) Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^4\) Pooled standard error of the least square means.
Table 7. Least square means\(^1\) of finishing feed intake and efficiency for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item(^5)</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^6)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>DOF</td>
<td>143(^b)</td>
<td>170(^a)</td>
<td>145(^d)</td>
<td>170(^c)</td>
</tr>
<tr>
<td>Feed intake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed ADFI, kg DM per d</td>
<td>10.92</td>
<td>11.04</td>
<td>10.66</td>
<td>11.30</td>
</tr>
<tr>
<td>Observed ADFI, Mcal NE(_{g}) per d</td>
<td>12.64</td>
<td>12.77</td>
<td>12.45</td>
<td>12.96</td>
</tr>
<tr>
<td>Predicted ADFI, kg DM per d</td>
<td>11.16</td>
<td>10.83</td>
<td>11.10</td>
<td>10.90</td>
</tr>
<tr>
<td>Predicted ADFI, Mcal NE(_{g}) per d</td>
<td>12.91</td>
<td>12.52</td>
<td>12.86</td>
<td>12.59</td>
</tr>
<tr>
<td>Feed efficiency</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G:F, kg DM per kg BW gain</td>
<td>0.112</td>
<td>0.117</td>
<td>0.123(^c)</td>
<td>0.107(^d)</td>
</tr>
<tr>
<td>G:F, Mcal NE(_{g}) per kg BW gain</td>
<td>0.097</td>
<td>0.101</td>
<td>0.106(^c)</td>
<td>0.093(^d)</td>
</tr>
<tr>
<td>RFI, kg DM per d(^7)</td>
<td>-0.47(^d)</td>
<td>0.54(^c)</td>
<td>-0.84</td>
<td>0.91</td>
</tr>
<tr>
<td>RFI, Mcal NE(_{g}) per d(^7)</td>
<td>-0.25(^b)</td>
<td>0.28(^a)</td>
<td>-0.34</td>
<td>0.38</td>
</tr>
</tbody>
</table>

\(^{ab}\) Means within a factor comparison without a common superscript differ significantly (\(P < 0.01\)).

\(^{cd}\) Means within a factor comparison without a common superscript differ significantly (\(P < 0.05\)).

\(^1\) No weaning treatment x finishing treatment x sire breed, weaning treatment x finishing treatment or weaning treatment x sire breed interactions were observed (\(P \geq 0.10\)).

\(^2\) Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously un-supplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.

\(^3\) Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^4\) Sire breeds were Angus (ANG) and Simmental (SIM).

\(^5\) DOF = days on feed, and represents the total duration of the finishing phase, including the 42-d adaptation period and total duration of the feed intake measurement period; RFI = residual feed intake.

\(^6\) Pooled standard error of the least square means.

\(^7\) Finishing treatment x sire breed interaction (\(P < 0.01\)).
Table 8. Least square means\(^1\) of visceral organ mass\(^2\) for weaning treatment\(^3\), finishing treatment\(^4\) and sire breed\(^5\).

<table>
<thead>
<tr>
<th>Item, g per kg of shrunk BW</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^6)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>Heart</td>
<td>4.51</td>
<td>4.49</td>
<td>4.49</td>
<td>4.51</td>
</tr>
<tr>
<td>Lungs and trachea</td>
<td>6.13(^c)</td>
<td>5.61(^f)</td>
<td>6.20(^e)</td>
<td>5.54(^d)</td>
</tr>
<tr>
<td>Liver and gallbladder</td>
<td>12.81</td>
<td>12.70</td>
<td>12.66</td>
<td>12.86</td>
</tr>
<tr>
<td>Pancreas</td>
<td>1.34</td>
<td>1.01</td>
<td>1.28</td>
<td>1.07</td>
</tr>
<tr>
<td>Kidneys and bladder</td>
<td>2.03</td>
<td>2.04</td>
<td>2.05</td>
<td>2.02</td>
</tr>
<tr>
<td>Spleen</td>
<td>1.38</td>
<td>1.47</td>
<td>1.40</td>
<td>1.45</td>
</tr>
<tr>
<td>Rumen</td>
<td>16.24</td>
<td>16.26</td>
<td>16.34</td>
<td>16.17</td>
</tr>
<tr>
<td>Reticulum</td>
<td>1.81</td>
<td>1.77</td>
<td>1.83</td>
<td>1.75</td>
</tr>
<tr>
<td>Omasum</td>
<td>6.12</td>
<td>5.82</td>
<td>6.16</td>
<td>5.78</td>
</tr>
<tr>
<td>Abomasum</td>
<td>3.80</td>
<td>3.70</td>
<td>3.67</td>
<td>3.82</td>
</tr>
<tr>
<td>Combined small intestine(^7)</td>
<td>11.43</td>
<td>10.78</td>
<td>10.89</td>
<td>11.33</td>
</tr>
<tr>
<td>Duodenum</td>
<td>0.91</td>
<td>0.91</td>
<td>0.80</td>
<td>1.03</td>
</tr>
<tr>
<td>Jejunum and ileum</td>
<td>10.62</td>
<td>10.14</td>
<td>10.17</td>
<td>10.56</td>
</tr>
<tr>
<td>Combined large intestine(^8)</td>
<td>11.89</td>
<td>12.44</td>
<td>11.24(^b)</td>
<td>13.11(^a)</td>
</tr>
<tr>
<td>Cecum</td>
<td>0.72</td>
<td>0.75</td>
<td>0.75</td>
<td>0.72</td>
</tr>
<tr>
<td>Colon and Rectum</td>
<td>11.65</td>
<td>11.66</td>
<td>10.89(^f)</td>
<td>12.42(^e)</td>
</tr>
<tr>
<td>Combined total(^9)</td>
<td>81.60</td>
<td>80.13</td>
<td>80.73</td>
<td>81.00</td>
</tr>
</tbody>
</table>

\(^a,b\) Means within a factor comparison without a common superscript differ (\(P < 0.001\)).

\(^c,d\) Means within a factor comparison without a common superscript differ (\(P < 0.01\)).

\(^e,f\) Means within a factor comparison without a common superscript differ (\(P < 0.05\)).

\(^1\) No three- or two-way interactions between weaning treatment, finishing treatment or sire breed were observed (\(P \geq 0.10\)).

\(^2\) Visceral organs were removed, separated, stripped, trimmed, rinsed, allowed to drip-dry and weighed immediately following harvest.

\(^3\) Weaning treatments were early weaned (EW; weaned at an average of 111 d of age and provided \(ad\) \(libitum\) access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.

\(^4\) Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^5\) Sire breeds were Angus (ANG) and Simmental (SIM).

\(^6\) Pooled standard error of the least square means.

\(^7\) Combined small intestine = duodenum + jejunum and ileum.

\(^8\) Combined large intestine = cecum + colon and rectum.

\(^9\) Combined total = sum of all individual visceral organs.
Table 9. Linear relationships between visceral organ mass\(^1\) and RFI\(^2\).

<table>
<thead>
<tr>
<th>Visceral organ</th>
<th>Slope</th>
<th>Intercept</th>
<th>(R^2)</th>
<th>(P)-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heart</td>
<td>0.37</td>
<td>-1.60</td>
<td>0.04</td>
<td>0.35</td>
</tr>
<tr>
<td>Lungs and trachea</td>
<td>-0.52</td>
<td>3.07</td>
<td>0.17</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Liver and gallbladder</td>
<td>0.12</td>
<td>-1.43</td>
<td>0.10</td>
<td>0.12</td>
</tr>
<tr>
<td>Pancreas</td>
<td>-0.01</td>
<td>0.01</td>
<td>&lt; 0.01</td>
<td>0.98</td>
</tr>
<tr>
<td>Kidneys and bladder</td>
<td>1.79</td>
<td>-3.68</td>
<td>0.22</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Spleen</td>
<td>-0.06</td>
<td>0.11</td>
<td>&lt; 0.01</td>
<td>0.93</td>
</tr>
<tr>
<td>Rumen</td>
<td>0.14</td>
<td>-2.27</td>
<td>0.13</td>
<td>0.07</td>
</tr>
<tr>
<td>Reticulum</td>
<td>0.29</td>
<td>-0.43</td>
<td>&lt; 0.01</td>
<td>0.64</td>
</tr>
<tr>
<td>Omasum</td>
<td>0.05</td>
<td>-0.26</td>
<td>&lt; 0.01</td>
<td>0.58</td>
</tr>
<tr>
<td>Abomasum</td>
<td>0.19</td>
<td>-0.65</td>
<td>0.04</td>
<td>0.31</td>
</tr>
<tr>
<td>Combined small intestine(^7)</td>
<td>0.17</td>
<td>-1.90</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>Duodenum</td>
<td>1.17</td>
<td>-1.06</td>
<td>0.17</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Jejunum and ileum</td>
<td>0.02</td>
<td>-0.24</td>
<td>&lt; 0.01</td>
<td>0.85</td>
</tr>
<tr>
<td>Combined large intestine(^8)</td>
<td>0.23</td>
<td>-2.75</td>
<td>0.19</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Cecum</td>
<td>0.66</td>
<td>-0.40</td>
<td>0.01</td>
<td>0.57</td>
</tr>
<tr>
<td>Colon and Rectum</td>
<td>0.28</td>
<td>-3.28</td>
<td>0.21</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Combined total(^9)</td>
<td>0.04</td>
<td>-3.48</td>
<td>0.17</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

\(^a,b\) Means within a factor comparison without a common superscript differ \((P < 0.001)\).
\(^c,d\) Means within a factor comparison without a common superscript differ \((P < 0.01)\).
\(^e,f\) Means within a factor comparison without a common superscript differ \((P < 0.05)\).

\(^1\) Visceral organs were removed, separated, stripped, trimmed, rinsed, allowed to drip-dry and weighed immediately following harvest. Mass was expressed on a g per kg of shrunk BW basis.

\(^2\) RFI = residual feed intake, expressed in Mcal of NE\(_2\) per d.
Table 10. Least square means\(^1\) of carcass measurements for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item(^5)</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^6)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>SFT(^7), cm</td>
<td>0.97</td>
<td>0.99</td>
<td>1.04</td>
<td>0.91</td>
</tr>
<tr>
<td>HCW, kg</td>
<td>378.01</td>
<td>382.29</td>
<td>379.31</td>
<td>381.00</td>
</tr>
<tr>
<td>REA, square cm</td>
<td>85.16</td>
<td>81.23</td>
<td>84.19</td>
<td>82.19</td>
</tr>
<tr>
<td>DP, %</td>
<td>63.09(^c)</td>
<td>61.70(^d)</td>
<td>62.36</td>
<td>62.43</td>
</tr>
<tr>
<td>KPH, %</td>
<td>2.84</td>
<td>2.66</td>
<td>2.81</td>
<td>2.69</td>
</tr>
<tr>
<td>YG</td>
<td>2.96</td>
<td>3.17</td>
<td>3.06</td>
<td>3.06</td>
</tr>
<tr>
<td>MS(^8)</td>
<td>740(^f)</td>
<td>681(^d)</td>
<td>779(^a)</td>
<td>642(^b)</td>
</tr>
</tbody>
</table>

\(^{a,b}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.0001)\).
\(^{c,d}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.01)\).
\(^{e,f}\)Means within a factor comparison without a common superscript differ significantly \((P < 0.05)\).

\(^1\)No weaning treatment x finishing treatment x sire breed, weaning treatment x finishing treatment or weaning treatment x sire breed interactions were observed \((P \geq 0.37)\).
\(^2\)Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.
\(^3\)Finishing treatments were high corn (HC; consisted of 69 % of DM from steam-flaked corn) and low corn (LC; iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).
\(^4\)Sire breeds were Angus (ANG) and Simmental (SIM).
\(^5\)SFT = 12\(^{th}\)-rib subcutaneous fat thickness, HCW = hot carcass weight, REA = ribeye area, DP = dressing percent, YG = USDA yield grade and MS = marbling score.
\(^6\)Pooled standard error of the least square means.
\(^7\)Tendency toward a finishing treatment x sire breed interaction \((P = 0.05)\).
\(^8\)600 = modest\(^0\), 700 = moderate\(^0\), 800 = slightly abundant\(^0\).
Chapter IV: Alternative weaning and finishing strategies for beef steers II: Effects on physical meat quality characteristics and consumer sensory perception

Jason K. Smith

ABSTRACT

Beef producers continuously search for alternative nutritional management strategies that enhance production efficiency and profitability. However, alternative management practices often affect beef product quality. An experiment was conducted to evaluate the effects of an alternative weaning and an alternative finishing strategy on physical meat quality characteristics and consumer perception of sensory attributes of retail beef products. Ribeye steaks were obtained from carcasses from experiment 2, which included two weaning treatments [early (EW) and conventionally weaned (CW)], two finishing treatments [high corn (HC; 69 % of finishing DM from steam-flaked corn) and low corn (LC; 50 % of finishing DM from steam-flaked corn iso-calorically replaced with dried corn gluten feed DCGF)], and two sire breeds [Angus (ANG) and Simmental (SIM)]. Steaks were analyzed to objectively evaluate physical meat quality characteristics, and were subjectively evaluated by trained consumer panelists to evaluate initial and overall tenderness, flavor intensity, juiciness and off-flavor, and by un-trained consumer panelists to evaluate texture, flavor, juiciness and overall acceptability. Mixed model ANOVA of a 2 x 2 x 2 factorial design revealed that early weaning increased cross-sectional muscle fiber area ($P < 0.001$) and tended to increase Warner-bratzler shear force (WBSF; $P = 0.08$), which were also greater for SIM than ANG steers ($P < 0.05$ and $P < 0.01$, respectively). When combined with an interaction between weaning treatment and finishing treatment for cooking
loss ($P < 0.05$), these effects likely led to an interaction between weaning treatment and finishing treatment that was observed for trained consumer perception of overall tenderness ($P < 0.05$) and a series of interactions between weaning treatment and sire breed as well as finishing treatment and sire breed that were observed for overall juiciness ($P < 0.01$ and $P < 0.05$, respectively). However no interaction or main effects of weaning treatment, finishing treatment or sire breed were observed for un-trained consumer perception of texture ($P \geq 0.14$), flavor ($P \geq 0.25$), juiciness ($P \geq 0.55$) or overall acceptability ($P \geq 0.34$). Collectively, the results of this experiment indicate that although alternative nutritional management strategies affect physical meat quality characteristics, the magnitude of these effects is not great enough to affect consumer sensory perception of retail beef products.

**INTRODUCTION**

Beef producers continuously seek alternative nutritional management strategies that decrease their dependency upon forages during times of limited abundance, as well as corn grain during times of increased competition from other industries. Early weaning (Peterson et al., 1987; Llewellyn et al., 2013) and the replacement of corn with coproducts of the corn milling industry (Hersom et al., 2010) are two strategies that have shown promise as alternatives to more conventional nutritional management strategies, and are often employed by producers during times of necessity. Eating satisfaction has been identified as one of the top three concerns of consumers and priorities for beef producers in the U.S. (NCBA, 2012). Distiller’s dried grains with solubles have been successfully utilized in finishing rations as an alternative to corn with positive effects on consumer perception of tenderness (Depenbusch et al., 2009). However, levels above 35 % of dietary DM have been shown to negatively affect beef product color and
retail shelf-life (Buttrey et al., 2013). Dried corn gluten feed, however, is a coproduct that is often a more readily available and economical option for producers in the Eastern U.S., and differs from distiller’s dried grains with solubles in nutrient composition. While the long-term inclusion of 25 % of dietary DM from dried corn gluten feed in backgrounding and finishing rations has been shown to maintain beef product quality (Segers et al., 2011), experiments evaluating the effects of inclusion at levels exceeding 25 % are lacking. Based upon these voids in the literature, an experiment was conducted to determine the effects of early weaning and isocaloric replacement of 50 % of finishing DM from steam-flaked corn with dried corn gluten feed on physical meat quality characteristics, as well as trained- and un-trained consumer sensory perception of sensory attributes from retail beef products.

**MATERIALS AND METHODS**

All procedures reported herein that involved live animals were approved by the Virginia Tech Institutional Animal Care and Use Committee. Additionally, all procedures that involved human subjects for the trained and un-trained consumer sensory evaluations were approved by the University of Georgia and Virginia Tech Institutional Review Boards, respectively.

**Cattle and management**

The cattle utilized in this experiment, treatment designations and experimental design were previously described in experiment 2. In brief, ANG (n = 16) and SIM (n = 12) sired steers were stratified by BW and sire breed before being randomly assigned to one of two weaning treatment groups [EW (n = 14) or CW (n = 14)] at approximately 106 d of age. Early weaned steers were weaned at an average age of 111 d and transported to a dry lot where they were provided *ad libitum* access to a concentrate and limit-fed cool season grass hay for 122 d.
Throughout this time, CW steers remained unsupplemented with their dams until being weaned at an average age of 233 d. All steers were then commingled and backgrounded on pasture for 190 d before being stratified by weaning treatment, sire breed and BW, and randomly assigned to one of two finishing treatments [HC (consisted of 69 % of DM from steam-flaked corn) or LC (50 % of DM from steam-flaked corn was iso-calorically and iso-nitrogenously replaced with dried corn gluten feed)]. Steers were randomly placed in one of four pens in a covered feedlot and adapted to a respective final finishing ration (Table 1). Steers were finished for an average of 157 d before being harvested at the Virginia Tech Meat Science Center (Blacksburg, VA 24061) in one of six groups upon reaching an ultrasound-estimated 12th-rib subcutaneous fat thickness (SFT) endpoint of 1.0 cm.

After a 24-h chilling period at 4° C, a 3-in section of the rib eye between the cranial side of the 10th and caudal side of the 12th rib was removed from the right side of each carcass and manually sliced into three ribeye steaks. Each of the three steaks was then designated to be used for proximate composition and histological analysis (steak 1), a trained consumer sensory panel evaluation (steak 2), or an un-trained consumer sensory panel evaluation (steak 3). At this time, duplicate LM samples (1.9-cm x 1.9-cm x 1.9-cm cubes) were collected from the medial portion of the LM from each steak designated for proximate composition and histological analysis. Cubes were embedded in optimum cutting temperature tissue freezing medium (NEG 50; Thermo Fisher Scientific Inc., Waltham, MA 02451), frozen on dry ice, and stored at -80°C until further processing. All steaks were then individually labeled, vacuum-sealed, frozen and stored at -20°C until further analysis.
Histology

Three transverse cryosections (10µm) from each duplicated LM sample were collected perpendicularly to the longitudinal orientation of the muscle fiber on 75 mm x 25 mm electrostatically charged microscope slides (Superfrost plus; Thermo Fisher Scientific Inc.) Cryosections were fixed for 10 min via submersion in paraformaldehyde and washed three times with PBS. Non-specific antigen sites were blocked with 5% horse serum in PBS and permeabilized with 0.5% nonionic detergent solution (Triton X-100 Surfact-Amps; Thermo Fisher Scientific Inc.) in PBS for 30 min at ambient temperature before being washed three times with PBS. Sections were then incubated for 60 min with fluorescent stains [4,4-difluoro-1,3,5,7,8-pentamethyl-4-bora-3a,4a-diaza-s-indacene (BODIPY 493/503, 1:400; Thermo Fisher Scientific Inc.) for detection of intramyocellular lipid droplets, wheat germ agglutinin Alexa Fluor 594 conjugate (1:400; Thermo Fisher Scientific Inc.) for visualization of the muscle fiber membrane, and 4',6-diamidino-2-phenylindole (DAPI, 1:1000; Thermo Fisher Scientific Inc.) for identification of nuclei] which were all prepared using the manufacturer’s instructions. Following three washes with PBS, coverslips were mounted to slides using anti-fade mounting medium (Prolong Gold antifade reagent; Thermo Fisher Scientific Inc.). Slides were then stored at 4°C until imaging. Images of each LM section were captured in triplicate (9 images per duplicated sample; 18 images per steer) at 10X magnification using an inverted fluorescent imaging microscope (Ti-E Eclipse; Nikon Inc., Melville, NY 11747) equipped with a camera control unit (DS-L3; Nikon Inc.). Image analysis software (NIS-Elements AR v.4.12.00; Nikon Inc.) was used to measure cross-sectional muscle fiber area (expressed in µm²) and to quantify intramyocellular lipid droplets (expressed in droplets per mm²). A minimum of 1000 muscle
fibers were measured per steer, and care was taken to exclude intramuscular fat depots and partial muscle fibers located in the perimeter of the field of view from all measurements.

**Colorimetry and proximate composition**

Frozen steaks used for colorimetric and proximate analysis were thawed at 4°C for 48 h prior to analysis. Three CIE luminance (L*), redness (a*) and yellowness (b*) color space measurements were obtained from each steak using a Minolta Chromo Meter (CR-310, Konica Minolta Sensing Americas, Inc., Ramsey, NJ 07446) calibrated with a white tile, which were then averaged for each steer. Following completion of the colorimetric analysis, four 2-g LM subsamples collected from each ribeye steak were individually powdered in liquid nitrogen in order to determine proximate chemical composition. Two powdered LM samples from each steer were freeze-dried for 72 h to determine moisture content prior to 10-h lipid extraction via chloroform:methanol (87:13) in a Soxhlet apparatus using the procedures described by Novakofski et al. (1989). Lipid-extracted samples were then freeze-dried for an additional 24-h prior to determining lipid content by difference. In order to determine protein content, the remaining two powdered LM samples were solubilized in a slightly acidic solution (pH = 6.8) that contained 8 M urea, 2 M thiourea, 3% SDS w/v, 75 mM dithiothreitol, and 0.05 M Tris-HCl using the procedure described by Warren et al. (2003). Solubilized samples were then heated to 95°C for 5 min before being analyzed to determine protein content with a commercially available reducing agent and detergent compatible colorimetric protein assay (Bio-Rad RC DC Protein Assay; Bio-Rad Laboratories, Inc., Hercules, CA 94547) using the instructions provided by the manufacturer. All samples were analyzed within a single microplate, and the intra-assay CV was 5.40%.
Frozen steaks utilized for the trained consumer sensory panel were weighed, thawed at 4°C for 18 h, and reweighed immediately prior to cooking in order to determine thaw loss. Thermocouples (Omega Engineering, Inc., Stanford, CT 06907) attached to a digital thermometer (Digi-Sense 12 channel scanning thermometer; Cole-Parmer, Vernon Hills, IL 60061) were inserted into the geometric center of each steak and used to monitor internal temperature. Steaks were placed on preheated open-hearth broilers, inverted once upon reaching an internal temperature of 35°C, and removed at an internal temperature of 69°C in order to achieve a final internal cooked temperature of 71°C (AMSA, 1995). Cooked steaks were then weighed to determine cooking loss, enclosed in aluminum foil, and allowed to rest for 5 min beneath a heat lamp. Following the 5-min resting period, steaks were sliced into ≤ 2.54 cm (height) x 1.27 cm (width) x 1.27 cm (length) samples and immediately placed in the original aluminum foil that contained the remaining cooking purge under the heat lamp. Duplicate samples were loaded into pre-warmed yogurt makers (Euro Cuisine Inc., Commerce, CA 90040) to maintain a constant temperature, and offered to each panelist under red lighting. Over a series of four sessions (one morning and one afternoon session per d occurring over two d), with seven randomly selected steaks represented at each session, trained panelists (University of Georgia personnel) evaluated and rated each sample on an eight-point hedonic scale for initial and overall tenderness (8 = extremely tender and 1 = extremely tough), beef flavor intensity (8 = extremely intense and 1 = extremely bland), juiciness (8 = extremely juicy and 1 = extremely dry), and off-flavor (8 = extremely intense, 1 = extremely mild and 0 = none detected).
Frozen steaks were thawed at 4°C for 48 h prior to being placed on preheated clamshell grills (George Foreman Model GR144; Applica Consumer Products, Inc., Miramar, FL 33027). Internal temperature was monitored using handheld digital thermometers. Steaks were inverted once upon reaching an internal temperature of 35°C, and removed from the grill upon reaching an internal temperature of 69°C in order to achieve a final cooked temperature of 71°C. Steaks were immediately sliced into 1.27-cm x 1.27-cm x 1.27-cm cubes and placed in re-sealable plastic bags, which were then sealed and submerged in a warm water bath (~ 60°C) where the cubes remained until removal for offering. Completed over a series of two sessions, with fourteen randomly selected steaks represented at each session, un-trained consumer panelists (Virginia Tech faculty, staff, students and community visitors) evaluated each sample in an individual booth under red lighting and rated samples on a nine-point hedonic scale (9 = like extremely and 1 = dislike extremely) for texture, juiciness, flavor and overall acceptability. Each panelist (n = 126) received a total of four samples (one sample from each weaning treatment x finishing treatment combination), and sample order was randomized to prevent order bias. A minimum of 14 observations for each sensory attribute were collected for each steak, and the average rating for each steak was used for analysis.

The remaining portion (approximately ½) of each cooked steak was refrigerated at 4°C for 24 h in re-sealable plastic bags and used to determine WBSF. Samples were removed from refrigeration and allowed to reach ambient temperature for 1 h. Six 1.27-cm diameter cores were then removed from each steak using a handheld coring device and ensuring that the orientation of the device remained parallel to the longitudinal orientation of the muscle fibers. Each core was sheared perpendicularly to the longitudinal orientation of the muscle fibers using an Instron.
Universal Testing Machine (Dual Column Model 3365, Instron Corp., Norwood, MA) equipped with a Warner-Bratzler shear head to determine maximum shear force, which was averaged for each steer.

**Statistical analyses**

All statistical analyses were conducted using JMP Pro v.11 (SAS Institute Inc., Cary, NC 27513), and steer was considered the experimental unit. Mixed model ANOVA was conducted via the Fit Model procedure to determine the fixed interaction and main effects of weaning treatment, finishing treatment and sire breed in a 2x2x2 factorial design. All initial statistical models included sire nested within sire breed as a random effect. Day was also included as a random effect for WBSF, thawing loss, cooking loss and for all sensory attributes of the trained and un-trained consumer panels. In addition, panelist and time (morning or afternoon) were included as random effects for sensory attributes of the trained consumer panel. Equality of variance and normality of data resulting from the mixed-model ANOVA were verified by plotting residual by predicted values for each individual response variable. Plots of residual by predicted values were also used to visually detect potential outliers. No more than two observations within each individual response variable were identified as outliers and subsequently removed from further analysis. Final statistical models were reduced in a step-wise fashion to remove statistically insignificant interaction effects, however the main effects of weaning treatment, finishing treatment and sire breed remained in all final models. Least square means were generated through ordered difference reports and separated using the Tukey-Kramer honestly significant difference method. All interaction and main effects were considered statistically significant at $P < 0.05$, considered as having a tendency toward significance at $P \geq 0.05$ and $< 0.10$, and considered statistically insignificant at $P > 0.10$. 

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RESULTS AND DISCUSSION

**Physical meat quality characteristics**

Least square means of weaning treatment, finishing treatment and sire breed for physical meat quality characteristics are reported in Table 2. No three- or two-way interactions between weaning treatment, finishing treatment or sire breed were observed for histological measurements, chemical composition, color, or WBSF ($P \geq 0.21$). Although intramyocellular lipid abundance was unaffected by weaning treatment ($P = 0.46$), finishing treatment ($P = 0.27$) or sire breed ($P = 0.80$), early weaning resulted in a 28% increase in cross-sectional muscle fiber area ($P < 0.001$). Postnatal muscle hypertrophy occurs as the result of a net increase in protein deposition over degradation due to satellite cell proliferation, differentiation and fusion to an existing myotube, which has been shown to be the result of IGF-I-induced signaling (Oksbjerg et al., 2004). Secretion of IGF-I in growing cattle increases as a result of increased dietary energy density (Houseknecht et al., 1988), which is conversely related to growth rate (Breier et al., 1986). Based upon this, it is likely that the increased nutrient consumption of EW steers during the early post-weaning dry-lot feeding period resulted in a level of IGF-I secretion that exceeded that of their CW contemporaries. When combined with the increased plasma insulin concentrations of EW steers during this management phase in experiment 2, it is likely that an increased activation of both the IGF-I-mediated Akt/Protein kinase B and insulin-mediated mammalian target of rapamycin ($mTOR$) pathways led to muscle hypertrophy that resulted in the observed increase in cross-sectional muscle fiber area. Independent of the effects attributed to weaning treatment, muscle fibers in ribeye steaks from SIM steers had an 18% larger cross-sectional area than ANG steers ($P < 0.05$). Although no reports could be found that compared cross-sectional muscle fiber area of ANG to SIM steers, Johnston et al. (1975) reported a
numerically greater cross-sectional LM fiber area of Charolais than ANG steers, suggesting that a portion of the increase in lean muscle growth and ribeye area that is often observed for cattle of Continental breed influence may be attributed to muscle fiber area. Nonetheless, cross-sectional muscle fiber area in the current experiment was unaffected by replacement of finishing DM from corn with dried corn gluten feed \( (P = 0.26) \).

Barker-Neef et al. (2001) reported that early weaning resulted in a 3.5\%- reduction in luminance of ribeye steaks, without a corresponding increase in WBSF, potentially due in part by the low magnitude of the difference in luminance values. Although luminance \( (P = 0.21) \) and yellowness \( (P = 0.28) \) were not affected by weaning treatment in the present experiment, early weaning resulted in a 20 \% reduction in redness \( (P < 0.01) \) and a tendency toward a 36 \% increase in WBSF \( (P = 0.08) \), which is consistent with the report of Schoonmaker et al. (2004). Additionally, replacement of steam-flaked corn with dried corn gluten feed in finishing rations increased redness by 22 \% \( (P < 0.01) \) and tended to decrease luminance by 4 \% \( (P = 0.08) \), without affecting yellowness \( (P = 0.35) \). Furthermore, ribeye steaks of ANG steers had 3 and 4 \% higher luminance \( (P < 0.05) \) and yellowness \( (P < 0.01) \) values, respectively, than SIM steers, while redness was unaffected by sire breed \( (P = 0.36) \). Previous research has shown that luminance, redness and yellowness of beef LM are each conversely related to consumer perception of tenderness (Wulf et al., 1997), however the exact physiological mechanism responsible for this relationship remains unclear. Although unaffected by finishing treatment \( (P = 0.62) \), ribeye steak cores from ANG steers required 30 \% less force to shear than cores from SIM steers \( (P < 0.01) \), indicating a substantial increase in objective tenderness.

Chemical composition (moisture, protein and lipid content) did not differ across weaning treatments \( (P \geq 0.37) \), finishing treatments \( (P \geq 0.16) \) or sire breeds \( (P \geq 0.71) \). Although not
surprising for moisture and protein content, after considering the differences in ultrasound-estimated IMF and carcass MS that were attributed to weaning and finishing treatments in experiment 2, it is likely that a relatively high intra-assay CV (14.79 %) contributed to the high SEM that led to the inability to detect differences in chemically-extracted lipid content. Furthermore, these results suggest that duplicate 2-g samples may not adequately reflect the relative lipid composition of beef LM.

Although no interaction or main effects of weaning treatment, finishing treatment or sire breed were observed for thawing loss ($P \geq 0.44$), an interaction between weaning treatment and finishing treatment existed for cooking loss ($P < 0.05$). Cooking loss was greater for ribeye steaks from EW HC than CW HC steers (18.39 vs. 12.64 %; SEM = 1.75; $P < 0.05$) and tended to be greater than CW LC steers (18.39 vs. 13.76 %; SEM = 1.75; $P = 0.05$), but was similar to EW LC steers (18.39 vs. 14.58 %; SEM = 1.75; $P = 0.16$). Independent of this interaction, cooking loss from ribeye steaks of ANG steers tended to be greater than SIM steers ($P = 0.09$). Although unclear, the interaction between weaning and finishing treatments, as well as the main effect of sire breed for cooking loss may have been a function of differences in intramuscular fat that were not detected by the means of chemical extraction that were utilized.

**Sensory attributes**

Least square means of weaning treatment, finishing treatment and sire breed for trained and un-trained consumer sensory attributes are reported in Table 3. No three-way interactions between weaning treatment, finishing treatment and sire breed were observed ($P \geq 0.59$) for consumer perception of any sensory attributes. Although unaffected by weaning treatment ($P = 0.15$) or finishing treatment ($P = 0.32$), trained panelists found the initial tenderness of ribeye steak samples from ANG steers to be greater than SIM steers ($P < 0.01$). Additionally, an
interaction between weaning treatment and finishing treatment existed for overall tenderness, as trained panelists found ribeye steak samples from EW LC steers to be less tender than CW LC (4.27 vs. 5.27; SEM = 0.27; $P < 0.01$) and CW HC (4.27 vs. 5.03; SEM = 0.27; $P < 0.05$) steers, and to tend to be less tender than EW HC steers (4.27 vs. 4.89; SEM = 0.27; $P = 0.06$), indicating an additive reduction in overall tenderness that resulted from a combination of early weaning and replacement of steam-flaked corn with dried corn gluten feed in the finishing ration.

Due to the moderate inverse correlations that exist between cross-sectional muscle fiber area and both initial and overall tenderness (Renand et al., 2001), it is possible that a combination of the increase in cross-sectional muscle fiber area that was observed for EW steers in the present experiment and the substantial reduction in carcass MS that resulted from corn replacement in experiment 2 were responsible for this interaction. In addition, overall tenderness was greater for ribeye steak samples from ANG than SIM steers ($P < 0.05$), which also may have been a function of a smaller cross-sectional muscle fiber area. Trained panelists also found ribeye steak samples from ANG steers to be more flavorful than SIM steers ($P < 0.001$), but detected no differences that could be attributed to weaning ($P = 0.29$) or finishing ($P = 0.52$) treatments. However both weaning treatment x sire breed ($P < 0.01$) and finishing treatment x sire breed ($P < 0.05$) interactions were observed for overall juiciness. Trained panelists found that ribeye steak samples from EW SIM steers were less juicy than EW ANG steers (4.13 vs. 4.96; SEM = 0.28; $P < 0.01$) and tended to be less juicy than samples from CW SIM (4.13 vs. 4.81; SEM = 0.28; $P = 0.07$) and CW ANG steers (4.13 vs. 4.71; SEM = 0.28; $P = 0.07$), which did not differ from one another ($P \geq 0.64$). Trained panelists also found that ribeye steak samples from LC SIM steers were less juicy than LC ANG steers (4.19 vs. 4.95; SEM = 0.24; $P < 0.01$) and tended to be less juicy than samples from HC ANG (4.19 vs. 4.73; SEM = 0.24; $P = 0.09$) and HC SIM
steers (4.19 vs. 4.76; SEM = 0.24; \( P = 0.09 \)), which did not differ from one another \((P \geq 0.74)\). Although marbling score was affected by weaning treatment and finishing treatment but not sire breed in experiment 2, the presence of these interactions is more consistent with the effects that were observed for cooking loss, indicating that a large portion of intramuscular fat may have been lost during the cooking process, thus leading to the perceived reduction in juiciness. This is further supported by the previously reported low correlation between marbling score and panelist perception of juiciness (Lorenzen et al., 2003). In addition, no interaction \((P \geq 0.20)\) or main effects of weaning treatment \((P = 0.81)\), finishing treatment \((P = 0.48)\) or sire breed \((P = 0.11)\) were observed for off-flavor.

In contrast to the results of the trained consumer sensory panel, no three- or two-way interactions between weaning treatment, finishing treatment and sire breed were observed for the un-trained consumer panel \((P \geq 0.14)\). On average, un-trained consumer panelists rated the texture, juiciness, flavor and overall acceptability as liked slightly to liked moderately, however these attributes were unaffected by weaning treatment \((P \geq 0.55)\), finishing treatment \((P \geq 0.57)\) and sire breed \((P \geq 0.25)\). Previous research indicated that un-trained consumer ratings of sensory attributes for retail beef products were, at most, lowly correlated with trained consumer ratings (Lorenzen et al., 2003), which may help to explain the inconsistency in results observed across the trained and un-trained consumer sensory evaluations in the current experiment. Nonetheless, these results suggest that although trained panelists were capable of detecting small differences in sensory attributes associated with early weaning and replacement of corn with dried corn gluten feed in finishing rations that were confounded by interactions with one another and sire breed, these differences were not detected by un-trained consumers. Based upon this, it
can be concluded that such alternative weaning and finishing strategies can be employed without affecting consumer sensory perception of ribeye steaks.

**CONCLUSIONS AND IMPLICATIONS**

Interpretation of the results reported herein suggests that early weaning, when proceeded by a short *ad libitum* concentrate feeding period prior to backgrounding increased cross-sectional muscle fiber area, reduces redness, and tended to increase WBSF of ribeye steaks, without affecting other major physical meat quality characteristics. Additionally, replacement of 50% of the finishing DM from steam-flaked corn with dried corn gluten feed increased redness, but tended to decrease luminance of ribeye steaks without affecting other major physical meat quality characteristics. Furthermore, a series of interactions were observed for cooking loss and trained consumer perception of sensory attributes that remain difficult to interpret. Nonetheless, the alternative nutritional management strategies reported herein had no effect on un-trained consumer perception of sensory attributes. Although these management strategies were shown to affect carcass characteristics in experiment 2 to a degree that would be expected to alter consumer perception, the absence of corresponding effects in this experiment suggest that these management options could be utilized without affecting un-trained consumer satisfaction.

**LITERATURE CITED**


Table 1. Average ingredient and nutrient composition\(^1\) of the final ration provided to steers during the finishing\(^2\) phase.

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Finishing treatment(^3)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HC</td>
<td>LC</td>
<td></td>
</tr>
<tr>
<td>Steam-flaked corn</td>
<td>68.65</td>
<td>33.89</td>
<td></td>
</tr>
<tr>
<td>Dried corn gluten feed</td>
<td>--</td>
<td>35.47</td>
<td></td>
</tr>
<tr>
<td>Wheat middlings</td>
<td>--</td>
<td>17.42</td>
<td></td>
</tr>
<tr>
<td>Cottonseed meal</td>
<td>11.10</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Corn silage</td>
<td>10.59</td>
<td>10.45</td>
<td></td>
</tr>
<tr>
<td>Cottonseed hulls</td>
<td>5.71</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Dicalcium phosphate</td>
<td>1.29</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Limestone</td>
<td>1.28</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Urea</td>
<td>1.00</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Salt</td>
<td>0.20</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>Trace mineral premix(^4)</td>
<td>0.09</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Vitamin E premix(^5)</td>
<td>0.04</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Selenium yeast(^6)</td>
<td>0.03</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Monensin(^7)</td>
<td>0.02</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>DM, % as-fed</td>
<td>71.60</td>
<td>73.55</td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>14.40</td>
<td>13.95</td>
<td></td>
</tr>
<tr>
<td>NDF</td>
<td>18.90</td>
<td>22.25</td>
<td></td>
</tr>
<tr>
<td>ADF</td>
<td>10.60</td>
<td>10.30</td>
<td></td>
</tr>
<tr>
<td>Ether extract</td>
<td>3.70</td>
<td>3.90</td>
<td></td>
</tr>
<tr>
<td>NE(_{\text{m}},) Mcal per kg</td>
<td>1.79</td>
<td>1.76</td>
<td></td>
</tr>
<tr>
<td>NE(_{\text{g}},) Mcal per kg</td>
<td>1.17</td>
<td>1.15</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Analyzed by an independent laboratory (Dairy One, Ithaca, NY 14850).
\(^2\) Commingled early (EW) and conventionally weaned (CW) steers were finished in a covered feedlot for an average of 157 d following a 190-d backgrounding period.
\(^3\) HC = high corn; LC = low corn.
\(^4\) Contained 5.15 % Zn, 2.86 % Mn, 1.80 % Cu and 0.18 % Co (Availa-4; Zinpro Corporation, Eden Prairie, MN 55344).
\(^5\) Contained 275,578 IU per kg of Vitamin E.
\(^6\) Contained 600 ppm Se (Sel-Plex 600; Alltech Inc., Nicholasville, KY 40356).
\(^7\) Type A medicated article; contained 200 g per kg of Monensin USP (Rumensin 90; Elanco Animal Health, Greenfield, IN 46140).
Table 2. Least square means\(^1\) of physical meat quality characteristics for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross-sectional muscle fiber area, (\mu m^2)</td>
<td>2976(^a)</td>
<td>2312(^b)</td>
<td>2743</td>
<td>2545</td>
</tr>
<tr>
<td>Intramyocellular lipid, droplets per (cm^2)</td>
<td>1.90</td>
<td>1.62</td>
<td>1.54</td>
<td>1.98</td>
</tr>
<tr>
<td>Chemical composition, % wet basis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moisture</td>
<td>73.29</td>
<td>73.71</td>
<td>73.40</td>
<td>73.59</td>
</tr>
<tr>
<td>Crude protein</td>
<td>18.12</td>
<td>18.88</td>
<td>20.04</td>
<td>16.95</td>
</tr>
<tr>
<td>Lipid</td>
<td>5.43</td>
<td>5.22</td>
<td>5.44</td>
<td>5.20</td>
</tr>
<tr>
<td>Color</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Luminance ((L^*))</td>
<td>37.31</td>
<td>36.32</td>
<td>37.53</td>
<td>36.10</td>
</tr>
<tr>
<td>Redness ((a^*))</td>
<td>10.92(^d)</td>
<td>13.04(^c)</td>
<td>10.77(^d)</td>
<td>13.19(^c)</td>
</tr>
<tr>
<td>Yellowness ((b^*))</td>
<td>8.97</td>
<td>8.69</td>
<td>8.96</td>
<td>8.71</td>
</tr>
<tr>
<td>WBSF, kg</td>
<td>4.12</td>
<td>3.02</td>
<td>3.42</td>
<td>3.73</td>
</tr>
<tr>
<td>Thawing loss, % wet basis</td>
<td>3.94</td>
<td>3.79</td>
<td>4.09</td>
<td>3.64</td>
</tr>
<tr>
<td>Cooking loss(^6), % wet basis</td>
<td>16.48</td>
<td>13.20</td>
<td>15.51</td>
<td>14.17</td>
</tr>
</tbody>
</table>

\(^a\)\(^b\) Means within a factor comparison without a common superscript differ \((P < 0.001)\).

\(^c\)\(^d\) Means within a factor comparison without a common superscript differ \((P < 0.01)\).

\(^e\)\(^f\) Means within a factor comparison without a common superscript differ \((P < 0.05)\).

\(^1\) No weaning treatment x finishing treatment x sire breed, weaning treatment x sire breed or finishing treatment x sire breed interactions were observed \((P \geq 0.21)\).

\(^2\) Weaning treatments were early weaned (EW; weaned at an average of 111 d of age, provided \textit{ad libitum} access to a concentrate-based ration and limit-fed mixed cool season grass hay at a rate of 0.68 kg per steer per d in a dry-lot setting for 122 d) and conventionally weaned (CW; previously unsupplemented and remained with dams until weaning at an average of 233 d of age). All steers were commingled and backgrounded in a grazing setting for 190 d prior to finishing.

\(^3\) Finishing treatments were high corn (HC: consisted of 69 % of DM from steam-flaked corn) and low corn (LC: iso-calorically and iso-nitrogenously replaced 50 % of DM from steam-flaked corn with dried corn gluten feed).

\(^4\) Sire breeds were Angus (ANG) and Simmental (SIM).

\(^5\) Pooled standard error of the least square means.

\(^6\) Weaning treatment x finishing treatment interaction \((P < 0.05)\).
Table 3. Least square means\(^1\) of sensory panel ratings for weaning treatment\(^2\), finishing treatment\(^3\) and sire breed\(^4\).

<table>
<thead>
<tr>
<th>Item</th>
<th>Weaning treatment</th>
<th>Finishing treatment</th>
<th>Sire breed</th>
<th>SEM(^5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EW</td>
<td>CW</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>Trained consumer panel(^6)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial tenderness</td>
<td>4.36</td>
<td>4.65</td>
<td>4.60</td>
<td>4.41</td>
</tr>
<tr>
<td>Overall tenderness(^7)</td>
<td>4.58</td>
<td>5.15</td>
<td>4.96</td>
<td>4.78</td>
</tr>
<tr>
<td>Beef flavor intensity</td>
<td>4.63</td>
<td>4.81</td>
<td>4.67</td>
<td>4.77</td>
</tr>
<tr>
<td>Overall juiciness(^8,9)</td>
<td>4.55</td>
<td>4.76</td>
<td>4.74</td>
<td>4.57</td>
</tr>
<tr>
<td>Off-flavor</td>
<td>1.26</td>
<td>1.30</td>
<td>1.25</td>
<td>1.32</td>
</tr>
<tr>
<td>Un-trained consumer panel(^10)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Texture</td>
<td>6.90</td>
<td>6.82</td>
<td>6.86</td>
<td>6.86</td>
</tr>
<tr>
<td>Flavor</td>
<td>6.78</td>
<td>6.86</td>
<td>6.79</td>
<td>6.85</td>
</tr>
<tr>
<td>Juiciness</td>
<td>6.85</td>
<td>6.74</td>
<td>6.82</td>
<td>6.77</td>
</tr>
<tr>
<td>Overall acceptability</td>
<td>7.00</td>
<td>6.94</td>
<td>7.02</td>
<td>6.92</td>
</tr>
</tbody>
</table>

\(^a,b\) Means within a factor comparison without a common superscript differ \((P < 0.001)\).
\(^c,d\) Means within a factor comparison without a common superscript differ \((P < 0.01)\).
\(^e,f\) Means within a factor comparison without a common superscript differ \((P < 0.05)\).
\(^1\) No weaning treatment x finishing treatment x sire breed interactions were observed \((P \geq 0.20)\).
\(^2\) Weaning treatments were early weaned \(\text{EW}; \text{weaned at an average of 111 d of age, provided}\ ad\ libitum\ access\ to\ a\ concentrate-based\ ration\ and\ limit-fed\ mixed\ cool\ season\ grass\ hay\ at\ a\ rate\ of\ 0.68\ kg\ per\ steer\ per\ d\ in\ a\ dry-lot\ setting\ for\ 122\ d\)\ and\ conventionally\ weaned \(\text{CW};\ previously\ unsupplemented\ and\ remained\ with\ dams\ until\ weaning\ at\ an\ average\ of\ 233\ d\ of\ age\)\. All\ steers\ were\ commingled\ and\ backgrounded\ in\ a\ grazing\ setting\ for\ 190\ d\ prior\ to\ finishing.
\(^3\) Finishing treatments were high corn \(\text{HC};\ consisted\ of\ 69\ %\ of\ DM\ from\ steam-flaked\ corn\) and low corn \(\text{LC};\ iso-calorically\ and\ iso-nitrogenously\ replaced\ 50\ %\ of\ DM\ from\ steam-flaked\ corn\ with\ dried\ corn\ gluten\ feed\)\.
\(^4\) Sire breeds were Angus \(\text{ANG}\) and Simmental \(\text{SIM}\)\.
\(^5\) Pooled standard error of the least square means.
\(^6\)Trained consumer panelists rated ribeye steak samples on an eight-point hedonic scale for initial and overall tenderness \((8 = \text{extremely tender and 1 = extremely tough})\), beef flavor intensity \((8 = \text{extremely intense and 1 = extremely bland})\), overall juiciness \((8 = \text{extremely juicy and 1 = extremely dry})\) and off-flavor \((8 = \text{extremely intense}, 1 = \text{extremely mild and 0 = none detected})\)\.
\(^7\) Weaning treatment x finishing treatment interaction \((P < 0.05)\).
\(^8\) Weaning treatment x sire breed interaction \((P < 0.01)\).
\(^9\) Finishing treatment x sire breed interaction \((P < 0.05)\).
\(^10\) Un-trained consumer panelists rated ribeye steak samples on a nine-point hedonic scale for texture, juiciness, flavor and overall acceptability; 9 = like extremely and 1 = dislike extremely.
Chapter V: Potential areas of future research

Jason K. Smith

Results of the research efforts reported herein have shed light to multiple areas of future research that would provide valuable information related to cattle management while providing a better understanding of the fundamental biology of cattle. One such area of research would be to evaluate the theory that metabolic imprinting is responsible for the effect of early weaning on marbling development. The results of experiments I and II warrant research to determine if marbling development is merely a function of total energy intake. This would require measuring lifetime nutrient intake after accounting for genetic variation, but would be a valuable first step toward better understanding the fundamental biology of marbling development. Although utilizing traditional beef cattle would be difficult and unfeasible from logistic and economic perspectives, utilizing beef cattle of dairy origin (i.e. Holstein steers) would be a suitable alternative. Another potential area of future research would be to evaluate the physiological significance of lung mass. Results of experiment II provided novel evidence of a relationship between lung mass and feed efficiency, and that nutritional management strategies affect lung mass at various postnatal stages of development. These findings warrant research to determine the role that the lungs play in feed efficiency. Due to the importance of oxygen to mitochondrial function and the cellular generation of energy, a plausible first step would be to determine if lung mass affects gaseous exchange. If the former is true, identifying the physiological significance of altered gaseous exchange would provide valuable information toward better understanding the fundamental biology of feed efficiency.