The Effects of Pre- and Postweaning Nutrition on Fertility and Feed Efficiency in Beef Heifers

A Thesis Presented in Partial Fulfillment of the Requirements for the Degree of Master of Science with a Major in Animal Science in the College of Graduate Studies University of Idaho by Maggie K. Bloomsburg

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AUTHORIZATION TO SUBMIT THESIS

This thesis of Maggie Bloomsburg, submitted for the degree of Master of Science with a Major in Animal Science and titled "The Effects of Pre- and Postweaning Nutrition on Fertility and Feed Efficiency in Beef Heifers," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Cattle in the Pacific Northwest graze a variety of forages which vary in quality. The effects of forage quality on heifer reproductive development and fertility is still under investigation. Therefore, the first objective was to investigate the effects of grazing different quality forages preweaning and postweaning on reproductive traits and feed efficiency in heifers. Although nutritional differences were present, pre- and postweaning treatments did not affect reproduction. This indicates different qualities of forage present in Idaho may be utilized for heifers. Feed costs represent a large portion of cattle producers' expenses. Selecting for feed efficiency allows producers to capitalize on these expenses. However, the effects of selecting for efficiency on reproduction are still undetermined. The second objective was to study the relationship between feed efficiency and reproductive development and fertility. No differences in reproductive traits were detected among heifers ranked as efficient, average or inefficient at utilizing feed for growth.

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LIST OF ABBREVIATIONS

AI	Artificial insemination
ADF	Acid detergent fiber
ADG	Average daily gain
AFC	Antral follicle count
AMH	Anti-Müllerian hormone
AMHRII	Anti-Müllerian hormone receptor II
ALF	Alfalfa pasture postweaning treatment
AP	Anterior pituitary
BCS	Body condition score
BEGWT	Weight at the beginning of postweaning treatment
BW	Body weight
BWT	Weight at end of postweaning treatment
cAMP	Cyclic adenosine monophosphate
CIDR	Controlled Internal Drug Release Insert
CL	Corpus luteum
СР	Crude protein
d	Day
DM	Dry matter
DMI	Dry matter intake
DOM	Digestible organic matter
E2	Estradiol
FSH	Follicle stimulating hormone
GnRH	Gonadotropin-releasing hormone
GRASS	Grass pasture postweaning treatment
h	Hour
IGF-1	Insulin-like growth factor-1
IRR	Irrigated pasture preweaning treatment
LH	Luteinizing hormone
MBW	Metabolic bodyweight at midpoint

min	Minute
mo	Month
mRNA	Messenger ribonucleic acid
NDF	Neutral detergent fiber
NE	Net energy
NIRS	Near-infrared spectroscopy
NMCREEC	Nancy M. Cummings Research, Extension and Education Center
NPY	Neuropeptide Y
$PGF_{2\alpha}$	Prostaglandin $F_{2\alpha}$
POMC	Proopiomelanocortin
PR	Pregnancy rate
RFI	Residual feed intake
RIA	Radioimmunoassay
RIBFT	Ribfat determined by ultrasound at the conclusion of feed trial
RNG	Range pasture preweaning treatment
RRCR	Rinker Rock Creek Ranch
RTS	Reproductive tract score
SNP	Single nucleotide polymorphism
UI IACUC	University of Idaho Institutional Animal Care and Use Committee
USWT	Weight at time of ultrasound and reproductive evaluation
wk	Week
WW	Weaning weight
yr	Year

CHAPTER 1: INTRODUCTION

Cattle and calves are the largest contributor to cash receipts in the national agricultural economy and the 2nd largest source of agricultural cash receipts in Idaho, producing \$78.2 billion and \$2 billion in 2015, respectively (USDA, 2016; USDA/ERS, 2018). In Idaho, cattle can graze a wide range of forage types and qualities, both between and within operations, and from year to year (Shewmaker and Bohle, 2010). Therefore, it is important to understand how these differences affect productivity as well as profitability.

Besides feed costs, reproductive failure within a herd also greatly impacts profit margins (Hall, 2013) and replacement heifer development represents a large investment for cow/calf operations. The decision to breed a heifer often involves keeping her until pregnancy is confirmed a couple months before the calving season. If pregnant, she still must raise her first calf to weaning before income is realized. Heifers that calve in the first 21 days of the calving season are more likely to have 3 to 5 calves during their productive lifetime (Cushman, et al., 2013). The management of replacement heifers can drastically affect profit margins for years and improving producers' ability to select replacement heifers for fertility and longevity is a valuable task. Therefore, understanding effects of environment and nutrition on heifer development and fertility is important.

Another consideration when choosing replacement heifers is increasing efficiency of the operation. One strategy is to select animals with greater feed efficiency to optimize returns from input costs. Using residual feed intake (RFI) to determine feed efficiency allows for selection of inherent efficiency and reduces selection pressure on other traits (Arthur and Herd, 2008). However, there is evidence that selecting for feed efficiency may have negative impacts on reproduction (Basarab et al., 2011; Shaffer et al., 2011). This is concerning because the most profitable replacement heifers are those calving early in the calving season (Cushman et al., 2013). However, only limited research exists on the effects of selecting for RFI on reproductive development and fertility.

This thesis offers a review of literature as well as two studies conducted to further understand factors involved in heifer development and fertility. Effects of nutritional differences before and after weaning on reproductive maturity and fertility were investigated as well as differences in fertility measures among heifers divergent in feed efficiency.

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CHAPTER 2: REVIEW OF LITERATURE

Cattle Management in Idaho

Cattle management in Idaho and the Pacific Northwest is diverse, with unique challenges for producers in different areas. Idaho has many types of landscapes that cattle producers utilize for cow herds, ranging from landscapes dominated by sagebrush to landscapes with native grasses and forests, and areas receiving less than 10" of precipitation per year to areas receiving over 40" (Roselle et al., 2009). Cattle can also be grazed on irrigated pastures, crop residue, or cover crops or can be fed in drylots. Additionally, grazing distribution can often be affected by management decisions and affects nutrient density. As a result, nutrient availability can vary in both quality and density. The effects of these differences on replacement heifer development has been investigated but requires more research to fully understand.

Physiology of Pubertal Onset in Heifers

Attainment of puberty can be defined as age at first estrus (Martin et al., 1992), exhibition of normal cyclicity (Perry, 2012), or capability to support pregnancy (Senger, 2012). There are many ways to measure both age at puberty or pubertal status, and the method or definition used is dependent on the focus of the research. *Hormonal transition of puberty*

As reviewed by Senger (2012) in his book, pubertal attainment is a complex process. Gonadotropin-releasing hormone (GnRH), luteinizing hormone (LH), follicle stimulating hormone (FSH) and estradiol (E2) are key hormones involved in the attainment of puberty by the female. Gonadotropin-releasing hormone is produced and released by the hypothalamus and stimulates the release of LH and FSH by the anterior pituitary (AP). Both LH and FSH stimulate follicles on the ovary. Luteinizing hormone binds to G-protein coupled receptors on thecal cells and increases cAMP levels, stimulating the conversion of cholesterol to testosterone, as well as the complex process of ovulation of the follicle. Follicle stimulating hormone stimulates follicle recruitment and growth by binding to FSH G-protein coupled receptors on granulosa cells, upregulating cAMP and causing testosterone from the cal cells to be converted to E2. Through a feedback mechanism, E2 influences GnRH release from the hypothalamus.

Pubertal onset is initiated by an increase in pulsatile GnRH release which stimulates FSH and LH release, therefore increasing E2 secretion from the ovary. Two types of neurons release GnRH into the portal blood system and cause secretion of LH and FSH from the AP. First, neurons that cause a surge release of GnRH make up the surge center and are responsible for LH surges and ovulation. These neurons respond positively to E2 stimulus and do not change in their sensitivity to E2 during the pubertal transition. Second, GnRH neurons responsible for regulating the tonic release of GnRH stimulate basal secretion of LH and FSH into the hypophyseal vein and into general circulation. These neurons respond negatively to E2 stimulus and are highly sensitive to circulating E2 prior to puberty; therefore, inhibiting frequent gonadotropic secretions. As the animal matures, the tonic center's sensitivity to E2 negative feedback decreases, allowing gonadotropins to be released at an increased frequency. This stimulates follicular development, and increased E2 production from follicles. The increased circulating estradiol by the dominant follicle stimulates the surge center release of GnRH, resulting in a surge of LH and subsequent ovulation. This initiates normal cyclicity. As the frequency of LH release increases in the peripubertal period, luteinization of follicular tissue may occur before the first ovulation. This production of progesterone is thought to help "prime" the brain for fully functional cyclicity in subsequent cycles (Schillo et al., 1992; Senger, 2012). The ability of GnRH neurons to release increased amounts of GnRH is dependent on their ability to fully respond to E2. This is influenced by many types of presynaptic neurons sending inhibitory or excitatory signals communicating cues from both the body and environment, including age and metabolic status of the animal (Senger, 2012; Amstalden et al., 2014). This complex network continues to be researched.

Effects of nutrition on puberty

Many studies have investigated patterns of gain in replacement heifers after weaning and effects on puberty and pregnancy rate (PR). Puberty occurs after heifers have obtained a certain physiological weight, but timing of development can be altered to decrease feed costs while still ensuring heifers are pubertal before the breeding season (Funston et al., 2012; Hall, 2013). For example, stair-step diets can be used to delay weight gain and development in order to utilize cheaper feedstuffs after weaning until closer to the breeding season when nutrition is increased in order to facilitate pubertal attainment (Cardoso et al., 2014). Many studies have also investigated appropriate bodyweight at the start of the breeding season. Heifers can be developed at a lower cost and still achieve acceptable PR when breed at 55 to 60% of mature body weight (BW), however, a longer breeding season may be needed (Funston et al., 2012). Age at puberty can be decreased and calving season shortened when heifers are developed to 60 to 65% of mature BW (Hall, 2013). This requires more input but may be more desirable for seedstock operations or smaller herds where calf crop uniformity is important.

Recent research indicates that timing of increased nutrition during the juvenile period is also important to age at puberty (Gasser, 2013; Amstalden et al., 2014). As reviewed by Amstalden and colleagues (2014), the release of GnRH is regulated by not only E2 negative feedback, but also metabolic-sensing pathways. Neuropeptide Y (NPY), proopiomelanocortin (POMC), and kisspeptin neurons in the hypothalamus influence sensitivity of the gonadotropin loop to E2 negative feedback. Leptin, a hormone released from adipose tissue, reduces NPY release and stimulates POMC neurons, signaling nutrient availability and prompting pubertal progression. On the other hand, when feed restriction occurs, NPY is released and inhibits GnRH release. The development of these hypothalamic pathways seems to be sensitive to nutritional differences occurring as early as 4 to 6.5 mo of age. Cardoso and colleagues (2014) conducted a study where heifers were fed an ad libitum concentrate diet from 4 to 6.5 mo of age, restricted to gain 0.35 kg/d until 9 mo, fed ad libitum high concentrate diet until 11.5 mo, then restricted until 14 mo. Heifers reached puberty by 12 mo, similar to the control group fed to gain 1 kg/d throughout the experiment. This juvenile development seems to prime hypothalamic pathways and accelerate puberty even when heifers are later restricted. In another study (Alves et al., 2015), proximity of NPY neurons to GnRH neurons and NPY expression were decreased in heifers at 8.5 mo of age on a high gain diet. In a subsequent study (Allen et al., 2017), heifers gaining 1 kg/d from 4 to 7.5 mo on either a high forage or high concentrate diet reached puberty at a similar age. Therefore, average daily gain during critical time points may be more important to manipulation of hypothalamic networks than dietary composition, allowing producers to utilize cheaper feedstuff. Together, these studies illustrate the importance of adequate

growth of heifers during critical times of hypothalamic development to ensure appropriate timing of puberty.

Calf nutrition during the early postnatal period can also be manipulated without early-weaning calves, which is often more feasible for cattle producers. When nursing calves were supplemented with concentrate, blood glucose and IGF-1 levels increased, and these increases were negatively correlated with age at puberty (Rodriguez-Sánchez et al., 2015). Age at puberty and potentially time of conception, is greatly influenced by preweaning growth. However, over-conditioning heifers can result in lighter offspring and lower reproductive performance in subsequent years (Funston et al., 2012). Increasing calf growth during specific periods may result in optimal timing of puberty (Gasser, 2013; Amstalden et al., 2014), which may also positively affect oocyte quality (Romar et al., 2011). Effects of early calf nutrition is difficult to research because nutrition is affected by environmental factors, such as forage quality and dam milking ability (Hall, 2013). Therefore, although juvenile nutrition of replacement heifers is often challenging to intensively manage, research investigating effects of forage quality grazed during the preweaning period on heifer development is warranted.

Measuring Reproductive Competence

Heifer pubertal status as well as measures of fertility can be evaluated before the breeding season to cull sub-fertile individuals. Evaluating pubertal status identifies animals that are cycling or are close to attaining normal cyclicity. Other measures can be used to evaluate the inherent fertility of heifers. These methods predict reproductive efficiency and longevity.

There are several methods to determine pubertal status that vary in labor, cost, skill required, and accuracy (Perry, 2012; Senger, 2012). Monitoring animals for estrus requires extensive labor but little other inputs. Display of estrus can be affected by environmental factors, such as weather, time of year, and pen cohorts, therefore, this method may not be as accurate as other methods. Cyclicity can be determined by measuring serum progesterone concentrations using commercial immunoassays. This requires multiple blood samples 7 to 10 days apart to determine the presence of a corpus luteum (CL), which indicates ovulation

has occurred. Blood progesterone values > 1 ng/mL indicates ovulation and thus cyclicity. This method is accurate but requires laboratory analysis and multiple animal handlings.

Assigning heifers reproductive tract scores (RTS) is another method to determine pubertal status (LeFever and Odde, 1986). Scores are assigned using either rectal palpation or ultrasonography. Size and tone of the reproductive tract and structures on the ovaries are used to assign a score of 1 to 5. Heifers receiving a RTS 1 or 2 are considered prepubertal. Animals receiving a RTS 3 are considered peripubertal, and those scored as a 4 or 5 are pubertal (LeFever and Odde, 1986; Martin et al., 1992). This method of screening heifers is repeatable between trained individuals (Rosenkrans and Hardin, 2002), and is indicative of a heifer's ability to become pregnant in various management scenarios, including artificial insemination (AI), natural service and synchronization protocols (Gutierrez et al., 2014). *Antral follicle count*

One emerging method to predict future fertility and potential longevity of heifers before the breeding season is to conduct antral follicle counts (AFC) via ultrasonography by counting all follicles \geq 3 mm in diameter on both ovaries (Burns et al., 2005; Ireland et al., 2008). Antral follicle counts are very repeatable between the follicular waves of the estrous cycle (Burns et al., 2005). Several studies (reviewed by Ireland et al., 2011) indicate relationships among AFC and reproductive performance.

A heifer is born with a limited supply of gametes called oocytes that are housed in primordial follicles. In contrast, bulls continually produce gametes throughout their lifetime (Senger, 2012). No or very little division of oocytes occurs after birth; therefore, the number of oocytes and primordial follicles present at any time in the ovary is dependent on the rate of degeneration (Monniaux et al., 2014). Primordial follicles can mature into primary, secondary, tertiary (or antral follicles), and preovulatory follicles. Alternatively, primordial follicles can remain un-activated. Follicles may undergo atresia at any stage. Cohorts of follicles mature in wave-like patterns (Senger, 2012). When antral follicles reach 3 to 5 mm (in bovine) they become part of a gonadotropin-sensitive pool of follicles and are visible to be counted using ultrasonography (Monniaux et al., 2014).

In 2008, Ireland and colleagues investigated the correlation between antral follicles \geq 3 mm and the primordial follicles present in the entire ovary in breeding-age heifers. Although there was a large variation among individuals, the greatest AFC obtained during the follicular wave was highly correlated (r = 0.90) to all types of follicles present on the excised ovary. Individuals with a high AFC also had the most primordial follicles. This study, along with an earlier study (Erickson, 1966), supports two hypotheses: 1) individuals with a larger ovarian reserve have longer fertile lifespans, 2) age-related infertility is due to exhaustion of the ovarian reserve. Whether AFC places a role in lifetime reproductive rates and profitability remains to be determined.

There are many physiological differences between cattle in different AFC categories. Three categories have been used for AFC in previous literature: low (\leq 15 follicles), average (15-24 follicles), and high (\geq 24 follicles; Ireland et al., 2008; Cushman et al., 2009). Cattle with low AFC have greater serum FSH concentrations (Burns et al., 2005), impaired luteal function, lower serum progesterone concentrations, impaired endometrial development during the luteal phase (Jimenez-Krassel et al., 2009), and reduced androgen production by thecal cells in response to LH (Mossa et al., 2010). These differences in the hormone milieu favor animals with high AFC over low AFC in reproductive success. Cattle with high AFC are better candidates for superovulation as the number of recovered embryos viable for transfer is greater compared to animals with low AFC (Ireland et al., 2007; Rico et al., 2009). Additionally, heifers with a high AFC are more likely to become pregnant (Cushman et al., 2009) and tend to calve earlier in the calving season, which increases longevity and profitability (McNeel and Cushman, 2015).

Applicability of determining AFC in replacement heifers as part of a pre-breeding screening method is dependent on two factors. First, AFC should be comparable between heifers at any stage of the estrous cycle. Second, AFC should be comparable between peripubertal and pubertal heifers. Cushman and colleagues (2009) concluded AFC can be performed during any stage of the estrous cycle in heifers without drastically AFC category after detecting a lower PR in low AFC heifers. However, research from another group (Burns et al., 2005; Ireland et al., 2007), shows variability in AFC throughout the estrous cycle in Holstein heifers and cows and beef heifers. It is also well-known that as the dominant follicle grows in diameter, it secretes inhibin, suppressing growth of other follicles (Senger, 2012). Additional research by McNeel and Cushman (2015) demonstrated differences in calving day in heifers with high and low AFC with ultrasonography done on a random day of the estrous cycle.

In prepubertal heifers, follicles grow in waves (Rawlings et al., 2003). The number of follicles in each wave is greater in mature animals than young calves (Evans et al., 1994a,b; Honaramooz et al., 2004), however, the number of follicles per wave seems to plateau before the peripubertal period (Evans et al., 1994a; Rawlings et al., 2003). This suggests that AFC performed on a group of peripubertal and pubertal heifers before the breeding season may not have an effect on the AFC score given. Further research validating AFC as a pre-breeding screening method is needed in multiple herds of varying genetic makeup.

Effects of nutrition on AFC

There is evidence that follicle numbers can be manipulated by nutritional signals. For example, the number of small follicles recruited can be increased by increasing the plane of nutrition before ovulation (Gutiérrez et al., 1997). There may also be windows of opportunity during development when nutrition influences the presence of primordial follicles and therefore reproductive longevity (Freetly et al., 2014).

Previous research indicates the ovarian reserve can be influenced during the fetal stage. Mossa and colleagues (2013) restricted yearling heifers to 60% of nutrient requirements during the first trimester. Female offspring showed no difference in fetal size, postnatal growth, or response to metabolic challenges. However, heifers from restricted mothers had a lower AFC and serum Anti-Müllerian hormone (AMH) levels both before and after puberty. In another study, Cushman and colleagues (2014) fed differing levels of nutrition to multiparous cows during the 2nd and 3rd trimester, restricting some cows to 75% of required nutrients in the 2nd and/or 3rd trimester. Despite deviations in cow weight and BCS, there were no differences in BW, ADG, age at puberty, or AFC in female offspring. However, heifers calving in the first 21 d of the calving season had a greater AFC. Together, these studies indicate the ovarian reserve may be more sensitive to nutritional availability during the 1st trimester when the gonads are developing than the 2nd and 3rd trimester, or severe nutrient restriction during gonad development may affect the ovarian reserve more than moderate nutrient restriction during the 2nd and 3rd trimester.

The degree to which AFC and depletion of the ovarian reserve is affected by postnatal nutritional differences is currently under investigation. Eborn and colleagues (2013) investigated the effect of a high-gain versus a low-gain diet from 8 to 15 months of age, during the peripubertal period, on AFC. Most heifers were pubertal at the time AFC was recorded. This study found no effect on the number of follicles due to dietary differences, but low AFC heifers were lighter in weight and gained less than high AFC heifers. Another study (Freetly et al., 2014) investigated the effect of a stair-step diet from 8.5 to 14 mo on the number of follicles. Heifers were restricted to gain 0.5 kg/d during the first 84 d and then compensated during the last 83 d to gain 0.9 kg/d or were held on a constant plane of nutrition. There was no difference in the number of antral follicles, yet restricted heifers had an increased number of primordial follicles in excised ovaries. In this study, diet composition was constant and differences in nutrition were obtained by restricting intake.

Another study by Amundson and colleagues (2015) examined the effects of nutritional differences on the ovarian reserve by observing changes in the population of primordial follicles by performing ovariectomies at various points of a stair-step versus control diet during the pre- and peripubertal period. Heifers on the restrictive diet had no difference in the number of primordial follicles present in the ovary over the course of the study. However, control heifers had fewer primordial follicles as they became pubertal. While there was no detected effect of treatment or time on AFC, the authors speculated that increased levels of nutrition may prompt the increased activation and atresia of follicles during the peripubertal period, potentially causing earlier exhaustion of the ovarian reserve and perhaps shortening the reproductive lifespan of a female. On the other hand, restricting feed to heifers during development may slow follicular activation and increase reproductive longevity. These researchers (Amundson et al., 2015) also detected a difference in SLIT2 mRNA in the ovary at 11 months of age between treatments. The SLIT-ROBO pathway has bee associated with follicular formation in the fetal ovary (Dickinson et al., 2010), however, its possible role in follicular activation and atresia in the postnatal ovary requires more investigation (Amundson et al., 2015). Furthermore, in a study observing ovaries from cattle of different ages, Erickson (1966) noted that the number and quality of primordial follicles (as indicated by chromatin configuration) began to decline around the peripubertal period. This could be related to increased activation around this time because the number of antral follicles was greatest before puberty at 180 days of age and then remained fairly stable until 10 years of age. These studies indicate the ovarian reserve may be sensitive to nutritional differences during the peripubertal period. Perhaps increased nutrition simply accelerated

activation and atresia of primordial follicles in the control treatment heifers during the trial while heifers in the stair-step diet underwent the same process over a longer period of time or at a later time in development (Freetly et al., 2014). The effect of these observed changes on the animal's future reproductive capabilities remains to be determined.

Anti-Müllerian hormone

Serum AMH is an indirect way to measure the number of total follicles within the ovary as well as healthy oocytes (Ireland et al., 2008; Rico et al., 2009) and is relatively constant throughout the follicular wave as well as between individuals within the same classification (Ireland et al., 2008). In heifers, AMH is mostly produced by granulosa cells of healthy follicles between 3- and 7 mm, which are classified as small to medium, and are gonadotropin-responsive (Rico, et al., 2009). As reviewed by Durlinger and colleagues (2002), the AMH receptor II (AMHRII) is expressed in both granulosa and thecal cells at a similar time as AMH expression. Anti-Müllerian hormone seems to be involved in regulating follicular development by inhibiting the initiation of primordial follicle growth. Therefore, when AMH expression is lower, the ovarian reserve is depleted more quickly. Thus, it appears that low AMH levels may be correlated to a smaller ovarian reserve and lower reproductive performance.

A long-term study (Jimenez-Krassel et al., 2015) provided stronger evidence that AFC and serum AMH concentrations are good predictors of fertility and longevity. Samples for serum AMH analysis were collected from Holstein heifers and later compared to the length of time the animal stayed in the herd as well as the reason the she was eventually culled. Heifers in the lowest quartile for AMH concentrations had shorter productive lives (time the animal was in the herd after her first calving) and were culled at a greater rate due to poor reproduction during their first lactation, contributing to an overall greater culling rate during the first lactation. These animals were also culled at a greater rate during the second lactation, indicating suboptimal fertility in this group. This study suggests there may be a threshold concentration of AMH and corresponding AFC at which animals have a much lower reproductive potential and should be replaced with more fertile and potentially more profitable individuals.

Ireland and colleagues (2009, 2011) found AMH levels to be relatively constant over one follicular wave in heifers, however, other researchers (Rico et al., 2010; Monniaux et al. 2013) found AMH to have a wavelike profile over the estrous cycle of dairy cows. This method is useful in research or to screen candidates for superovulatory treatment (Rico et al., 2009), but a lack of validation in multiple herds and lack of a well-developed assay (Ireland et al., 2008; Rico et al., 2009) prevent it from being appropriate for mainstream use at the present time.

Feed Efficiency and Fertility in Beef Heifers

Cattle producers have long attempted to monitor and quantify differences in efficiencies between animals. However, some measures of efficiency tend to select for animals that may have other undesirable traits such as increased frame size (Arthur and Herd, 2008). Therefore, researchers developed a system of measuring feed intake to quantify differences in feed efficiency. This is done by measuring daily feed intake and comparing it to expected intake based on weight gained during a feed trial. The difference between expected intake and actual intake is termed residual feed intake (RFI). Animals can be classified as inefficient, average, or efficient based on the number of standard deviations they lay from the average animal in the contemporary group (Welch et al., 2012). Animals with more negative values are considered more efficient while animals with more positive values are considered less efficient. (Arthur and Herd, 2008). Separating the herd into groups can be helpful both for research and for breeding animal selection. By design and definition, this measure is independent of other measurements of growth and measures inherent physiological differences in efficiency (Crews, 2005; Arthur and Herd, 2008; Herd and Arthur, 2009).

Relationship Between Feed Efficiency and Age at Puberty

Feed efficiency is moderately heritable (Arthur and Herd, 2008). There is evidence that heifers with greater feed efficiency have an increased age at puberty when using conventional methods to determine feed efficiency (Basarab et al., 2011; Shaffer et al., 2011). This physiological relationship is of interest to both researchers and producers. Basarab and colleagues (2011) speculated heifers obtaining puberty before or during an RFI trial have additional energy expenditure during estrus, which decreases their efficiency of weight gain. Additionally, Shaffer and colleagues (2011) theorized that earlier-maturing heifers have an increased intake of energy, which is in turn stored as fat, resulting in these heifers being categorized as less efficient. Efficient heifers also have greater circulating levels of non-esterified fatty acids, indicating a faster rate of fat breakdown and leaner body composition compared to less efficient heifers (Kelly et al., 2010). As discussed earlier, fat tissue is a source of permissive signals for pubertal attainment. Therefore, the relationship between feed efficiency, body fat, and age at puberty is important to understand.

In a 2013 review, Randel and Welsh, Jr., discussed this relationship and the physiological processes involved. Body fat plays an important role in pubertal attainment and research has shown efficient heifers can have 2 to 5% less body fat than inefficient heifers. Additionally, protein accretion associated with growth requires less energy than fat deposition, making immature animals more efficient than mature animals. Therefore, efficient heifers may require more feed and additional days on feed to reach the physiological fatness required for them to obtain puberty. Basarab and colleagues (2011) investigated the relationship between RFI and age at puberty by adjusting RFI for backfat in an attempt to remove the effects of fatness on differences in age of puberty. When adjusted for backfat, efficient heifers reached puberty 13 d later than inefficient heifers.

This is important for producers to be aware of, as both age at puberty (Cushman and Perry, 2012) and feed efficiency have shown to be moderately heritable (Arthur and Herd, 2008). However, because there are large variations in age at puberty (Shaffer et al., 2011) and other factors to consider in replacement heifer selection, such as age at calving and pounds of calves weaned (Basarab et al., 2011), producers should be able to include RFI ranking in their selection criteria.

Relationship Between Feed Efficiency and Fertility

There is limited research directly examining the relationship between feed efficiency and fertility. However, there are many overlapping of factors related to both feed and reproductive efficiency.

Body condition score is a visual appraisal of fat stores and available excess nutrients. It is established that BCS is a good indicator of future reproductive success (Morrison, et al. 1999; Hess et al., 2005). For example, a meta-analysis illustrated that length of anestrus after calving was negatively correlated to BCS (Hess et al., 2005). Fat stores can be affected by nutrient availability and efficiency of nutrient utilization (Basarab et al., 2012). Therefore, increases in efficiency should allow for greater nutrient availability for reproductive processes.

Another possible link between feed efficiency and reproductive success is IGF-1. This metabolic hormone seems to be both a permissive signal to the rise in LH as well as a regulator of ovarian activity (Hess et al., 2005; Basarab et al., 2012). Although IGF-1 is undoubtedly involved in metabolic processes inherently affecting feed efficiency, serum IGF-1 levels do not accurately predict feed efficiency (Basarab et al., 2012; Randel and Welsh, Jr., 2013).

Limited studies have also investigated pregnancy rates among heifers and cows of varying feed efficiencies. In 2007, Basarab and colleagues reported a greater twinning rate among cows producing inefficient calves. In 2004, Echternkamp and colleagues noted a greater number of follicles in cattle selected to have twins. Together, these two studies suggest a possible link between increased number of follicles, greater fertility (Ireland et al., 2008; Cushman et al., 2009) and feed efficiency. However, it is possible differences in feed efficiency as yearlings among progeny were the result of the effects of uterine environment and nutrient restriction (Du et al., 2010). In 2011, Basarab and colleagues reported a lower PR in efficient heifers as well as a delay in pregnancy. These heifers had a 15% lower PR by d 27 of the breeding season, even when using backfat as an adjustment factor. This trend was similar in cows producing efficient progeny, who calved 5 to 6 d later than cows producing inefficient progeny (Basarab et al., 2007). Research further examining interactions between feed efficiency are important to profitability (Hall, 2013).

CHAPTER 3: OBJECTIVES

Cattle in Idaho and the Pacific Northwest can be exposed to a variety of forage types and landscapes. The quality of these forages varies by species, time of year, weather patterns and available water. Utilizing economical feedstuffs is important to cattle producers, as feed costs represent the largest cost to cattlemen. Another substantial cost is developing replacement heifers. Considerable research has been conducted to determine the most economical management strategies to develop heifers in a way that maximizes lifetime profit. It has been established that producers can utilize cheaper feedstuffs earlier in the development period and later capitalize on compensatory growth, allowing heifers to still reach puberty before the breeding season. However, more recent studies have investigated early life development and the effects of nutrition in different stages of life on reproduction. Reproductive success is dependent on both a heifer's sexual maturity and her inherent fertility. Sexual maturity can be determined using RTS, while AFC is a measure of inherent fertility. Critical time points in development for both maturity and fertility are being established, as well as the degree of nutritional differences needed to detect differences in reproduction.

Another challenge facing cattle producers is rising feed costs. One way to capitalize on input costs is to select for more efficient animals. However, selecting cattle for efficiency can be challenging as selecting animals for bodyweight or ADG can increase herd frame score. Using RFI to determine feed efficiency allows for selection of inherent efficiency and reduces selection pressure on other traits. However, there is evidence that selecting for feed efficiency may have negative impacts on reproduction. This would be detrimental to cattle producers' profit. However, there is only limited research on the effects of selecting for RFI on reproductive development and fertility. Research performed here utilized RTS and AFC because these traits are indicative of heifer fertility and longevity. These traits are also moderately heritable when compared to pubertal status at synchronization and PR.

The goal of the research discussed in this thesis is to add to the body of knowledge on impacts of early life nutrition and feed efficiency at one year of age on fertility in beef heifers.

Experiment 1 (Chapter 4)

The first objective of this study was to determine differences in forage quality and heifer growth between two preweaning and two postweaning environments. The preweaning environments were either irrigated pasture in Carmen, Idaho or rangeland in Hailey, Idaho. The postweaning environments were either mixed grass pastures or predominantly alfalfa pastures. The second objective was to investigate the effect of preweaning and postweaning environment, as well as their interactions, on measures of reproductive development and fertility in heifers. These measures included RTS, AFC, pubertal status at synchronization, AI PR and final PR. The experimental hypothesis was that nutritional differences would exist between treatments and result in differences in bodyweight and ADG among heifers. An additional hypothesis was that early life nutritional differences would not affect the reproductive and fertility measures used in this study.

An additional objective of this study was to perform a preliminary investigation on the effects of pre- and postweaning environment on feed efficiency. Heifers in the abovementioned environments were placed on a feed trial and evaluated for feed efficiency. The proportion of heifers from each environment within an RFI classification was then determined. The experimental hypothesis was that pre- or postweaning treatments would not differ in the proportion of heifers that were ranked inefficient, average or efficient. *Experiment 2 (Chapter 5)*

The first objective of this study was to investigate reproductive differences among heifers of differing feed efficiencies. Heifers on a feed efficiency trial were evaluated for reproductive and fertility measures including RTS, AFC, pubertal status at synchronization, AI PR and final PR. Then, the proportion of heifers achieving differing AFC and RTS scores was compared across RFI categories. The proportion of heifers achieving puberty and pregnancy was also compared among RFI categories. The second objective was to investigate the relationships between RFI components and reproductive measures. It was hypothesized that proportions of heifers achieving various AFC and RTS scores would not differ among RFI categories and RFI components would not affect reproductive measures.

Figure 3.1 is a schematic overview of both Experiment 1 and Experiment 2 to provide clarification of the timeline and experimental designs.

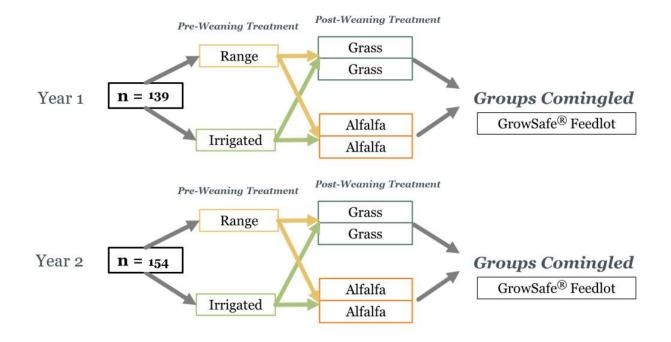


Figure 3.1. Schematic overview of Experiment 1 and Experiment 2 taking place over 2 years.

CHAPTER 4: EFFECTS OF PRE- AND POSTWEANING NUTRITION ON FERTILITY IN BEEF HEIFERS

ABSTRACT

The objective of this study was to investigate the effects of pre- and postweaning forage grazing on heifer development and fertility. Crossbred heifers (n = 293) grazed irrigated (IRR) or rangeland (RNG) pasture with dams from 89.5 ± 0.9 d of age until weaning at 209.5 ± 0.9 d of age. Fecal samples were collected for NIRS analysis in yr 2. Weaned heifers then strip-grazed on alfalfa (ALF) or grass (GRASS) pastures for 56 d in yr 1 and 61 d in yr 2 with 2 replicates per treatment in both years. Heifers were weighed every 2 wk and forage samples were collected for wet chemistry analysis. After grazing, all heifers were managed similarly. At 10 d before estrous synchronization, heifers weighed $383.3 \pm$ 5.9 kg, and reproductive tract score (RTS) and antral follicle count (AFC) were determined by ultrasonography. Heifers were synchronized using the 14 d CIDR AI protocol 10 d later. In yr 1, serum progesterone concentrations were determined at ultrasonography and synchronization. Heifers were considered pubertal when progesterone concentration was > 1 ng/mL. Pregnancy rate (PR) to AI and final PR was determined by ultrasound. A mixed model was used to determine effects of forage, time, and their interactions on diet composition and treatment effects on heifer bodyweight, ADG, RTS and AFC. Correlations between variables were also tested. Crude protein (CP) content was affected by forage \times time interaction in the preweaning treatment. There was no difference in CP content in mid-July (P > 0.05), but CP in IRR was 4.1 ± 0.59 % greater (P < 0.01) than RNG at time of weaning. Weaning weight was not affected by treatment, but IRR calves tended (P = 0.10) to gain 0.1 kg/d more than RNG calves and were 18 kg heavier (P = 0.03) than RNG calves after the postweaning treatment. Postweaning, CP content was affected (P < 0.05) by forage in yr 1 and 2 and averaged 15.5% and 16.6% of dry matter for ALF and 8.9% and 8.7% for GRASS in yr 1 and 2, respectively. Although ALF heifers gained more than GRASS heifers $(0.38 \pm 0.05 \text{ vs.} 0.17 \pm 0.05 \text{ kg/d}; P = 0.02)$, postweaning treatment did not affect (P > 0.05) BW. Body weight at weaning and at ultrasound were correlated with RTS, regardless of

treatment (r = 0.29 and 0.31, respectively, P < 0.01). Preweaning or postweaning treatment did not affect (P > 0.05) pubertal status as measured by progesterone, PR, AFC, or RTS. There was a tendency (P = 0.10) for RTS to affect AFC. In summary, despite differences in growth rates, replacement heifers grazing either irrigated or range pastures while nursing, and alfalfa or grass pastures after weaning, did not differ in fertility measures.

INTRODUCTION

The cow/calf industry plays a vital role in the economy of Idaho and the Pacific Northwest, creating \$2 billion worth of cash receipts in Idaho in 2015 (USDA/ERS, 2018). In addition, cattle graze a variety of lands in Idaho, most of which are not suitable for farming (Shewmaker and Bohle, 2010). Utilizing these feed sources aid in reducing feed costs, which is the largest non-fixed cost in most beef operations (Hall, 2013). However, differences in forage quality have the potential to affect replacement heifer development as forage-based diets are common both while nursing and after weaning.

Besides feed, heifers and cows that fail to produce a calf represent a large cost to beef producers (Hall, 2013). Therefore, selecting sexually mature and fertile replacement heifers is imperative to profit margins. Reproductive tract scores are a practical option for beef producers to evaluate sexual maturity of replacement heifers (LeFever and Odde, 1986; Kasimanickam et al., 2016). By evaluating the size and tone of the reproductive tract and structures on the ovaries, heifers can be classified by pubertal status and either culled or estrous synchronized based on sexual maturity (Kasimanickam et al., 2016). Antral follicle counts are an indicator of an individual's ovarian reserve and potential reproductive lifespan (Ireland et al., 2008; McNeel and Cushman, 2015; Jimenez-Krassel et al., 2015). Performing AFC on replacement heifers before the breeding season allows potential selection for heifers more likely to calve in the first 21 d of the calving season (McNeel and Cushman, 2015).

There is considerable evidence that nutritional differences both before weaning and from weaning to breeding can affect sexual maturity (Day et al., 1986; Buskirk et al., 1995; Gasser, 2013). There is also evidence that an individual's inherent fertility as measured by the number of antral and primordial follicles present in the ovaries can be affected by

nutritional differences (Freetly et al., 2014; Amundson, et al., 2015). However, the stage of development that is most sensitive to nutritional changes is still under investigation.

Both sexual maturity at the beginning of the breeding season and inherent fertility are important to PR of replacement heifers. Understanding how nutritional differences affect reproduction at various times of development can aid in management decisions and increase profit margins.

OBJECTIVES AND HYPOTHESES

The objectives of this study were: 1) to evaluate the effects of changes in dietary quality before weaning and after weaning on heifer reproductive development and fertility, and 2) to investigate the effects of preweaning and postweaning environment on feed efficiency as a yearling heifer. The null hypotheses tested were: 1) preweaning and/or postweaning environment would not affect reproductive measures, and 2) preweaning and/or postweaning environment would not affect RFI category.

MATERIALS AND METHODS

All procedures were approved by the UI IACUC protocol numbers #2016-56 and #2015-19.

Grazing treatments

Crossbred heifers were subjected to different management practices common in the Pacific Northwest during the preweaning and postweaning grazing periods (yr 1: n=139, yr 2: n=170) in a 2 × 2 factorial design study. All pairs were managed similarly from calving to mid-May (89.5 ± 0.9 d of age). At this time, heifers with their dams were grazed either on irrigated pasture (IRR) in Carmen, Idaho at UI Nancy M. Cummings Research, Extension and Education Center (NMCREEC; 45°17'09" N, 113°53'19" W) or rangeland (RNG) in Hailey, Idaho at Rinker Rock Creek Ranch (RRCR; 43°20'39"N, 114°22'32"W) for 4 mo. Orchardgrass (*Dactylis lomerate*), Quackgrass (*Elymus repens*), Smooth Bromegrass (*Bromus inermis*) and Red Clover (*Trifoluim pretense*) were the predominate species in IRR whereas RNG was sagebrush steppe with species Great Basin Wildrye (*Leymus cinereus*),

Columbia Needlegrass (*Achnatherum nelsonii*), Beardless Bluebunch Wheatgrass (*Pseudoroegneria spicata*), Sandberg Bluegrass (*Poa secunda*), and Squirreltail (*Elymus elymoides*), predominating, with Cheatgrass (*Bromus tectorum*) utilized in the early grazing season.

Heifers were fence-line weaned in mid-September. Heifers remained at their respective locations until assigned to postweaning treatment (yr 1 = 10/19/16; yr 2 = 10/20/17). While on the postweaning treatment, heifers grazed Orchardgrass and Bromegrass mix (GRASS) or alfalfa (ALF) pastures at NMCREEC for 58 d in yr 1 and 61 d in yr 2. Pastures were replicated within years and heifers were stratified between the four pastures by preweaning treatment and BW. Grass pastures were standing forage, but alfalfa pastures were swathed due to ranch management considerations.

Heifers were weighed in the morning at the beginning and end of trial over 2 consecutive days and every 2 wk during the trial. In yr 2, heifers in the ALF treatment were fed alfalfa hay beginning 35 d into treatment due to pasture shortages. After treatment, in yr 1, all heifers were fed grass hay for 2 wk in their grazing paddocks before being transitioned to a drylot. In yr 2, heifers from forage replicates were combined and continued to receive either grass or alfalfa hay according to treatment group until moving to the drylot. In the drylot, heifers were combined and placed into 4 pens based on BW. Heifers were treated similarly for the rest of the trial.

Feed efficiency trial

After a transition period, heifers underwent a feed efficiency trial (yr 1: 1/24/16 to 4/12/16; yr 2: 1/16/17 to 4/12/17) using the GrowSafe system (GrowSafe, Calgary, Alberta, Canada). Heifers (yr 1: n = 139; age = 342.3 ± 1.4; start BW = 320.7 kg ± 2.9; end BW = 414.7 ± 3.0; yr 2: n = 154; age = 331.9 ± 1.2; start BW = 312.5 kg ± 2.4; end BW = 412.1 ± 2.9) were placed into 4 pens each equipped with 5 feeding nodes at NMCREEC. Pen assignment was by BW to ensure heifers were in a pen with contemporaries of a similar BW. Residual feed intake (RFI) was determined over a 77 and 85 d period in yr 1 and 2, respectively. Heifers were weighed over 2 consecutive d at the initiation and conclusion of the trial. Heifers were also weighed every 2 wk during the study. Ultrasound backfat was determined at the conclusion of the trial and used in RFI calculations. Heifers were fed a diet of 80% alfalfa hay, 10% wheat middlings, and 10% liquid supplement (PerforMix Nutrition,

Nampa, ID; Table 4.1). All diets were prepared daily as a total mixed ration and fed *ad libitum*. Daily feed samples were collected and dried to obtain dry matter (DM) percentage. This was used to determine daily dry matter intake (DMI) for feed efficiency calculation. Daily feed samples were composited into 2 time periods and components analyzed (Cumberland Valley Analytical Services, Inc., Waynesboro, PA) to give an estimate of diet quality. Diets in both years averaged 87.5% DM, 13.5% CP, 1.18 Mcal/kg NEm, and 0.62 Mcal/kg Neg.

Diet quality

To estimate dietary quality of preweaning treatments, in yr 2, fecal samples were collected from 10 random heifers in each treatment in mid-July and at weaning and analyzed using near-infrared spectroscopy (NIRS) with a Midwest Great Plains dataset (D. R. Tolleson, Sonora A&M Agrilife Research Center, Sonora, TX and Grazingland Animal Nutrition Lab, Temple TX). No preweaning diet estimates were obtained in yr 1.

To estimate dietary quality of postweaning treatments, forage samples were collected from grass and alfalfa pastures. In yr 1, 3 to 5 forage samples were taken when heifers arrived on pastures, mid-way through the postweaning treatment and when heifers left the pastures as well as of supplemental hay. In yr 2, 5 forage samples were collected every 2 wk of the grazing period. In yr 1, forage samples were analyzed separately, and values averaged after analysis to determine pasture means. In yr 2, forage samples were dried separately and then combined by pasture and time of sample. A sub-sample was used for further analysis.

In yr 1, forage samples were weighed, dried, and ground (Retsch, Verder Scientific, Inc., Newtown, PA) through a 4 mm screen before being ground through a 2 mm screen. Forage availability was calculated. Wet chemistry analysis was conducted to determine dry matter (DM), organic matter, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin and nitrogen content. Dry matter and organic matter analyses were done sequentially. Samples were weighed (1.8-2.2 g) into crucibles in duplicate. Samples were then placed in a drying oven at 135°C for 2 h, cooled to room temperature and weighed for DM analysis within 1 h. Samples were then placed in a muffle oven and ashed at 600°C overnight, cooled and weighed within 1 h.

Neutral detergent fiber, ADF and lignin analyses were done sequentially. Samples were weighed out into Ankom[®] filter bags in duplicates and weighed 0.45-0.55g. Samples

were placed in an Ankom[®] digestion vessel with 2 L of neutral detergent solution, 20 g of sodium sulfite, and 4 ml of alpha amylase and heated and agitated for 1 h. Samples were washed and agitated twice with boiling water and 4 mL of alpha amylase and once with boiling water for 5 min each. Bags were then removed, washed with acetone for 3 min, dried for 100°C for 2 h and weighed within 1 h of removal. Samples were then processed for ADF following the same procedure using acid detergent solution and washing samples 3 times for 3 min each using only boiling water. After drying, samples were then weighed for ADF calculations. For lignin content, samples were re-dried, placed in Daisy Incubator[®] jars with 500 mL of 72% Sulfuric acid (H₂SO₄) and rotated for 3 h. Bags were rinsed with water until the pH of bags was neutral and then rinsed for 3 min with acetone, dried and weighed.

Nitrogen samples were weighed (0.45-0.55 g) in duplicate. Blanks and controls of 0.15 g of Ammonium Sulfate and 0.5 g of Acetinilide were included with each run. Two Kjeltac[®] tablets and 15 mL of sulfuric acid were added as a catalyst to each tube. Tubes were place in a digestion vessel for 90 min, cooled and titrated for analysis of nitrogen content by a Foss[®] machine.

In yr 2, after dry matter was determined at NMCREEC, forage samples were sent to a remote lab (Cumberland Valley Analytical Services, Inc., Waynesboro, PA) for wet chemistry analysis of CP, ADF, NDF and ash.

Reproductive data

Ten d before estrous synchronization, RTS were determined for all heifers (n = 293 yr 1: n = 139; yr 2: n = 154). Reproductive tract scores were performed via palpation and verified by ultrasound. Briefly, RTS 1 to 5 were assigned, with tracts receiving a 1 and 2 score being considered prepubertal, tracts receiving a 3 score being considered peripubertal, and tracts receiving a 4 and 5 score being considered pubertal (Martin et al., 1992). Antral follicle count was determined by scanning ovaries using an Ibex, EVO portable ultrasound (E. I. Medical Imaging, Loveland, CO). In yr 1, a 7.5 MHz linear probe was used and in yr 2, a 6.5 MHz linear probe was used. Videos were recorded of each ovary and later used to count follicles \geq 3 mm as established by Ireland and colleagues (2008) and Cushman and colleagues (2009). Heifers were determined to be low (< 15 follicles), medium (15-24 follicles) or high (\geq 25 follicles). On the day of ultrasonography, heifers were classified as low, medium, or high based on visual observations. A subset of heifers (n = 80; n = 20 from

each treatment) was selected for AFC in yr 1. Heifers > 431 kg, < 299 kg, as well as heifers born in April were not selected. Angus- and Hereford-sired heifers were selected with priority because herd management dictates these heifers will be retained and therefore can be used for long-term research and evaluation. Heifers sired by SimAngus sires were randomly selected to fill remaining slots. In yr 2, AFC was determined for all heifers (n = 154) to increase statistical power. Data from 7 heifers in yr 1 and 7 heifers in yr 2 were lost due to recording issues.

To determine pubertal status at the initiation of synchronization, coccygeal venipuncture blood samples were collected into 10 mL non-heparinized vacutainer tubes (Vacutainer, Becton, Dickinson and Company, Franklin Lakes, NJ) 10 d or 9 d before initiation of estrous synchronization, and the day of synchronization immediately before CIDR insertion. Blood was allowed to clot for 24 h at 4°C and was centrifuged at $2500 \times g$ (4°C) for 30 min, and serum collected and stored at -20°C. Samples from yr 1 were used for progesterone analysis using a double antibody radioimmunoassay (RIA; MP Biomedicals, Costa Mesa, CA). All samples were analyzed in duplicate and the intra-assay coefficient of variation was 6.4%. Heifers with at least one sample with progesterone concentrations greater than 1 ng/mL were considered pubertal.

Estrous synchronization

Heifers were estrous synchronized using the 14-day CIDR protocol (Thomas et al., 2014). Briefly, on d 0, heifers received a CIDR (Zoetis, Parsippany, NJ) device. Fourteen d later, the CIDR was removed. On d 33, heifers received PGF_{2α} (Lutalyse, 25 mg i.m.; Zoetis, Parsippany, NJ), and EstroTect patches (Rockway Inc., Spring Valley, WI) were applied to aid with detection of estrus. Between d 33 and 36, heifers were monitored for estrus using patches and visual observation 3 times daily by 2 trained observers. Sixty-six h after PGF_{2α}, all heifers displaying estrus were bred using AI by 1 of 3 inseminators. In yr 1, heifers were bred using Split-Time AI and heifers not expressing estrus were monitored for estrus and inseminated 24 h later. Heifers not displaying estrus by 90 h after CIDR removal received GnRH (Factrel, 100 μ g i.m., Zoetis, Parsippany, NJ) at the time of AI. In yr 2, all heifers were bred 66 h after CIDR removal, with heifers not displaying estrus receiving an injection of GnRH. Heifers were stratified based on treatment, RTS, and BCS and were bred with 1 of 3 bulls each year with either conventional (n = 128) or sexed (n = 162) semen. Bulls were

placed with heifers 14 d after timed AI for the remainder of the 45 d breeding season. To determine AI and final PR, blood pregnancy specific protein B levels were tested 30 d (BioPyrn; BioTracking, Inc., Moscow, Idaho) after AI, and pregnancy status determined by rectal ultrasonography 42, 64, and by rectal palpation, 142 d after AI.

Statistical analysis

Statistical analysis was performed using SAS (9.4 version). In the preweaning treatment, dietary quality was investigated using a mixed model to determine the effects of treatment, time and their interaction. In the postweaning treatment, a mixed model using repeated measures was used to determine effects of forage, time, and their interaction on diet composition. A mixed model was used to determine effects of preweaning and postweaning treatment and their interaction on bodyweight at weaning (WW), the end of postweaning treatment (BWT) and at ultrasonography (USWT), ADG, RTS, AFC and RFI. Replicate and the interaction between replicate, pre-, and postweaning treatment were offered as random variables. To determine the effect of pre- and postweaning treatment on RFI, heifer RFI was determined within year. Year datasets were combined for analysis. The relationship between RTS and AFC was also tested with a mixed model, with year as a random variable. Additionally, PROC GLIMMIX was used to determine effects of treatment on pubertal status and PR in yr 1. Correlations between dependent variables were also tested.

Chi-square analysis using SAS Proc FREQ was used to test for differences in proportions of heifers from different pre- and postweaning environments later classified as inefficient, average, and efficient heifers during the feed trial. For all analyses, significance was declared at $P \le 0.05$ and a statistical tendency declared at P > 0.05 and $P \le 0.10$.

To determine RFI, actual individual daily DMI was regressed against predicted intake based on ADG during the feeding period, using metabolic bodyweight at midpoint (MBW) and ultrasound ribfat (RIBFT) as adjustments. Heifers were ranked by RFI and classified as inefficient, average, or efficient based on the number of standard deviations from the mean of all heifers in the study (> 0.5 SD above mean, \pm 0.5 within SD, and < 0.5 SD, respectively). In yr 1, the following equation was used:

$$RFI = DMI - [-1.00079 + (0.13194 \times MBW) + (2.37991 \times ADG) + (0.05426 \times RIBFT)]$$

In yr 2, the following equation was used:

$$RFI = DMI - [0.24519 + (0.11884 \times MBW) + (0.87450 \times ADG) + (0.04555 \times RIBFT)]$$

RESULTS

Forage analysis

There was a location × time interaction (P < 0.01) on preweaning diet quality in yr 2 for fecal CP and DOM (Table 4.2). For fecal analysis, the H statistic, or Mahalanobis distance was 1.9 ± 0.1 for this dataset, which indicates the dataset chosen for calibration was acceptable (Tolleson and Schafer, 2014). There were no differences in CP in mid-July, when calves were assumed to be consuming a diet with a significant amount of forage. However, CP remained high in the IRR treatment and decreased in the RNG treatment by the time of weaning (P < 0.01). Digestible organic matter increased in the IRR treatment from mid-July to weaning and decreased in the RNG treatment (P < 0.01).

Postweaning forage quality was affected by forage type, time of sample, and the interaction. Nutrient analysis is provided in Figure 4.1. In yr 1, ADF was affected by the forage × time interaction (P = 0.03), however, NDF was not. Crude protein, lignin and ash were affected by forage type (P < 0.05). Crude protein was on average, 6.6% greater in ALF than GRASS. Lignin increased 6% in ALF but only 3% in GRASS.

In yr 2, DM was affected by the forage × time interaction (P < 0.02) and increased from 88.1% to 95.9% in ALF. Ash was affected by forage (P < 0.01). Neutral detergent fiber and ADF were affected by both forage ($P \le 0.02$) and time (P < 0.01) and remained greater in GRASS throughout treatment. Crude protein was affected by forage (P = 0.01) and was, on average, 7.9% lower in GRASS. Total digestible nutrients were affected by forage (P =0.02) and by time (P < 0.01) and were, on average, 5.7% lower in GRASS. Net energy maintenance and NEgain were affected by forage ($P \le 0.03$) and by time (P < 0.01) and NEgain was, on average, 0.17 Mcal/kg greater in ALF.

Body weight

No interactions between preweaning and postweaning treatment on heifer performance were detected in this study and therefore will not be presented or discussed. The effects of preweaning and postweaning treatments on growth and reproductive measures are presented in Table 4.3 and 4.4, respectively.

Preweaning treatment did not affect WW (IRR = 265.9 ± 3.7 kg, RNG = 251.8 ± 3.7 kg; P = 0.13). Grazing location tended to influence ADG from birth to weaning (IRR = 1.1 ± 0.02 kg/d, RNG = 1.0 ± 0.02 kg/d; P = 0.10).

Weaning weight and weight at the beginning of the postweaning treatment (BEGWT) was not different between ALF and GRASS treatments (P = 0.92 and P = 0.90, respectively) by design. There was a tendency for preweaning treatment to affect ADG during the postweaning treatment with RNG heifers gaining more than IRR heifers ($0.33 \pm 0.05 \text{ kg/d vs}$. $0.21 \pm 0.05 \text{ kg/d}$, respectively; P = 0.08). Heifers on ALF gained 0.21 kg/d more than GRASS heifers during the postweaning treatment (ALF = $0.38 \pm 0.05 \text{ kg/d}$, GRASS = $0.17 \pm 0.05 \text{ kg/d}$; P = 0.02). Postweaning treatment did not affect ENDWT (P = 0.22), however, preweaning location did affect ENDWT (IRR = 299.4 ± 5.8 ; RNG = 281.4 ± 5.8 ; P = 0.03) There was no difference in USWT between pre- or postweaning treatments. *Reproductive measures*

Preweaning or postweaning treatment did not affect AFC, RTS, AI PR or final PR (Table 4.3 and 4.4). In yr 1, pubertal status before synchronization (ALF = $47.8 \pm 0.1\%$, GRASS = $45.6 \pm 0.1\%$; *P* = 0.79) was not affected by postweaning treatment.

Weaning weight, BEGWT, ENDWT, and USWT were positively correlated with RTS (r = 0.29, r = 0.28, r = 0.33; r = 0.31, respectively, P < 0.01). Average daily gain from birth to weaning was lowly correlated with RTS (r = 0.22, P < 0.01). Also, ADG during postweaning treatment was lowly correlated with RTS (r = 0.13 P = 0.03)

There tended to be an effect of RTS on AFC (P = 0.10). Heifers with RTS 3 had more follicles than RTS 5 (P < 0.03) and tended to have more follicles than RTS 4 (P = 0.10).

Feed efficiency

Preweaning treatment tended to affect RFI value (P = 0.09) with IRR heifers receiving a more efficient score. There was also a tendency for differences in the proportion of IRR and RNG heifers that ranked inefficient, average, or efficient during the RFI trial (Fig. 4.2, P = 0.10). There was no effect of postweaning treatment on RFI or feed efficiency.

DISCUSSION

Reproductive measures

One purpose of this study was to investigate the effects of pre- and postweaning environment on measures of reproductive development and fertility. The dietary differences detected in this study did not affect reproduction as measured by AFC, RTS, pubertal status, or PR. Although limited differences were detected in bodyweight and ADG, this may be due to the limited number of replicates within the current study, as there were differences detected in the quality of diets.

Growth before weaning can play an influential role in future reproductive performance. It is likely this period of development is just as, if not more critical to future longevity than after weaning (Gasser et al., 2006; Gasser, 2013). The present study detected no differences in heifer weaning weight, despite differences in forage quality from 90 d of age to weaning and a tendency for greater ADG from birth to weaning in heifers grazing IRR before weaning. In yr 2, fecal samples analyzed by NIRS revealed an improvement in CP and DOM for the IRR compared to RNG treatment at the time of weaning in late summer. Numerical differences in WW suggest this difference in dietary quality at a time when calves are consuming mostly forage affected calf growth. Obtaining fecal samples allow some correction for selectivity that cannot be assessed with forage samples (Tolleson and Schafer, 2014). Although no statistical difference was detected, IRR calves were 14.1 kg heavier at weaning than RNG calves, which could be an economical advantage, if calves are sold at weaning. With additional years of data, this difference may become statistically different. It appears heifers from RNG were able to display compensatory growth during the postweaning treatment, as they tended to gain more than IRR heifers after weaning. However, RNG heifers were lighter than IRR heifers at the end of the postweaning

treatment. Additionally, although not statistically significant, heifers on RNG as calves were still 13.0 kg lighter at ultrasound, despite being in the feedlot with *ad libitum* consumption for 3 mo. This agrees with previous studies where weaning weight explained 47% of weight variation at the end of the backgrounding period (Robinson, et al., 2013). Other studies reported that cattle with restricted growth before weaning and lighter weaning weights were able to compensate partially with improved postweaning growth (Drouillard and Kuhl, 1999). However, preweaning growth-restricted calves finished at a lighter weight; though, these calves were grazed with their dams on endophytic-infected tall fescue (Drouillard and Kuhl, 1999). The current study is evidence that replacement heifers may be able to thrive on a variety of forage sources present in Idaho without noticeably affecting subsequent reproductive development or fertility.

Antral follicle count appears to be a viable indication of fertility (Ireland et al., 2008; Cushman et al., 2009) and cow longevity (McNeel and Cushman, 2015). Antral follicles ≥ 3 mm present on the ovaries is an indicator of the ovarian reserve, or the supply of gametes a female has available in her lifetime (Ireland et al., 2008). After birth, it is most likely that if this supply can be affected by management, it would be through the rate of degeneration (Monniaux et al, 2014). The degree to which this can be affected in early life and prepubertally remains to be determined. In the current study, no differences were seen in AFC between postweaning treatments, which took place at 8 to 10 mo of age, despite differences in ADG. This agrees with previous literature in which heifers were fed a high vs. low gain diet (0.8 vs 0.45 kg/d) for a longer period of time (8 to 15 months) and had no difference in AFC at breeding between treatments (Eborn et al., 2013). Therefore, it appears that moderate nutritional differences postweaning may not affect AFC at the time of breeding. Additional studies looking at single-step stairstep diet from 8 to 13 mo of age reported differences in primordial follicles at 13 mo of age (Freetly et al., 2014; Amundson et al., 2015) compared to the control group, indicating primordial follicles may be sensitive to nutritional changes. However, these heifers were not evaluated at breeding age. The AFC reported in the current study are lower than previously reported (Ireland et al., 2008; Cushman et al., 2009; Eborn et al., 2013) It is unclear why this occurred. Perhaps differences in breed composition or methods in determining AFC contributed to these differences (Ireland et al., 2008; Cushman et al., 2009). However, AFC may be a viable

decision-making tool for selecting replacement heifers, as it is simple to determine with training and could be used in select breeding evaluations.

Sexual maturity is reliably detected using RTS (LeFever and Odde, 1986). Reproductive tract scores are also an acceptable measure of longevity because of the relationship between cyclicity at the start of the breeding season, calving in the first 21 d and longevity (Gutierrez et al., 2014). With some training, RTS are simple to perform, even without an ultrasound machine, allowing them to be incorporated into some breeding programs (Rosenkrans and Hardin, 2002). The present study detected no differences in RTS associated with dietary treatments. Previous studies (Gasser et al., 2006; Roberts et al., 2009) indicate that preweaning and postweaning nutrition may influence sexual maturity. The aforementioned studies examined larger nutritional differences than were present in the current study. Gasser and colleagues (2006) examined large differences in protein and energy after early weaning or normal weaning calves and determined it is possible to accelerate puberty with early life changes. However, their studies involved large nutritional differences for longer lengths of time than those in the current study. Roberts and colleagues (2009) observed a tendency for a lower proportion of heifers to be pubertal at 14 mo when restricted to 80% of the control group's intake for 140 d after weaning. However, their study resulted in greater differences in ADG and BW than the current study. The RTS data are further supported by the pubertal and pregnancy data from yr 1 of the experiment, as well as AI PR in yr 1 and yr 2. However, limited conclusions should be made from pregnancy data in this study because the 14 d CIDR protocol is able to induce puberty in peripubertal heifers, which likely positively influences PR (Leitman et al., 2008).

Reproductive tract scores were correlated with bodyweights from weaning to time of evaluation. This is similar to other studies where RTS was correlated to bodyweight at prebreeding evaluation (Hall, 2005; Holm, et al., 2009). Furthermore, bodyweight and fatness are permissive signals to the initiation of puberty and cyclicity (Perry, 2016) and increases in gonadotropins cause an increase in follicle development and diameter (Senger, 2012).

There was a difference in AFC between heifers of differing RTS, with heifers given RTS 3 having more follicles than RTS 4 or 5. This could be due to several factors. Heifers with RTS 3 have 8 to 10 mm follicles present on the ovary, but no large dominant follicle. In contrast, heifers with RTS 4 have a large dominant follicle and heifers with RTS 5 have a CL (LeFever and Odde, 1986). As peripubertal heifers approach cyclicity, the decrease in sensitivity to negative estradiol feedback allows gonadotropins to increase, causing follicles to increase in diameter (Day and Anderson, 1998). However, as a large dominant follicle forms, it secretes inhibin and estradiol, which inhibits follicular growth (Senger, 2012). Therefore, it is possible heifers with large dominant follicles have a lower AFC due to hormonal regulation of follicles at this stage of the estrous cycle. Previous studies (Burns et al., 2005; Ireland et al., 2007) have demonstrated variability in AFC throughout the estrous cycle. In contrast, other studies (Cushman et al., 2009; McNeel and Cushman, 2015) have demonstrated AFC can be used in beef heifers as a measure of fertility without taking stage of the estrous cycle into consideration. It is also possible that large structures on the ovary inhibited counting of smaller follicles.

The nutritional differences created in this study did not affect reproductive development at the time of synchronization or PR. Many studies have investigated timing of nutritional differences and the effect on reproduction. In a 2014 study, heifers fed *ad libitum* from 4 to 6.5 mo and later restricted during the peripubertal period reached puberty at the same time as heifers fed to gain consistently from 4 mo to puberty (Cardoso et al., 2014). This and other studies (Alves et al., 2015; Allen et al., 2017) indicate development of the hypothalamic pathways during early life is important for normal pubertal attainment.

Nutrition during the prepubertal and peripubertal stage is important to timely pubertal attainment. Heifers with an increased ADG after weaning are more likely to become pubertal before the start of the breeding season (Buskirk et al., 1995). Restriction of growth to 0.21 kg/d during this time inhibited the rise of both serum LH concentration and LH pulse frequency, delaying puberty (Day et al., 1986). Although GRASS heifers gained 0.17 kg/d during the postweaning treatment, this period was only 60 d, and both ALF and GRASS heifers were able compensate gains when placed in the drylot. The current study was not able to determine age at pubertal onset; however, no differences were observed in the proportion of heifers classified as pubertal by serum progesterone in yr 1, or by RTS in yr 1 and 2, indicating that heifers from both treatments were adequately developed. Also, AI and final PR were acceptable. Timing of nutrition before the breeding season has been heavily researched. Grings and colleagues (2007) developed heifers to be 60 to 65% of their

mature body weight at the start of the breeding season. They found no difference in the proportion of heifers pubertal at the start of the breeding season among heifers weaned at different ages and undergoing different patterns of gain between weaning and breeding. Cardoso and colleagues (2014) restricted heifers from 6.5 to 9 mo and still achieved a desirable age at puberty. This, as well as the current study, indicates nutrition shortly after weaning, or 8 to 10 mo of age, may not be as critical to hypothalamic-gonadal and reproductive tract development as early life and the peripubertal period. *Feed efficiency*

Feed efficiency is an important trait to select for when choosing replacement heifers to maximize profit. However, because feed efficiency is challenging to measure on a large scale, it is difficult to determine how feed efficiency may be affected by early life. It is established that fetal development can affect later life performance, such as muscle:fat ratio and hot carcass weight (Du et al., 2010; Funston et al., 2010). In this study, a tendency was detected for a difference in RFI rankings among heifers raised on irrigated or range pastures during the preweaning treatment with more heifers from IRR treatment being ranked as efficient. This is in contrast to a study conducted by Cafe and colleagues (2009) in which heavy and low birthweight calves were raised to gain either 1 or 0.5 kg/d until weaning. There was no effect of preweaning growth on feed conversion ratio while in the feedlot. However, these animals entered the feedlot at 26 mo of age, therefore effects of preweaning growth may have dissipated during the backgrounding period. Further research investigating the effects of preweaning environment on not only feed efficiency during heifer development, but also throughout her lifetime is of economic importance. In the current study, heifers were gestated in the same environment as preweaning treatment group, therefore, it is difficult to speculate if the observed difference was from fetal or early life development.

This study detected no effect of postweaning treatment on feed efficiency. This agrees with a study conducted by Springman and colleagues (2017) where heifers developed after weaning for over 150 d on rangeland, corn residue, or in a drylot, had no differences in feed efficiency during their first pregnancy. However, Choat and colleagues (2003) observed steers backgrounded on native range to have a greater ADG:DMI ratio than steers backgrounded on winter wheat, due to compensatory weight gains. Taken together, the

mentioned studies support that nutritional differences earlier in life may have more of an effect on feed efficiency than differences in later life. The current study supports the need for additional research in this area.

Conclusions

Despite differences in dietary treatment and growth during the pre- and postweaning period, this study detected in no differences in reproductive performance as measured by RTS, AFC, pubertal status or PR in heifers. This study supports the economic value of raising heifers on lower quality feed to capitalize on compensatory growth after the grazing season. Additional research examining the effect of these grazing strategies on fetal development and reproductive measures would be valuable. Previous research indicates that it may be important to raise replacement heifers in similar conditions she will experience as a cow.

This study also supports the continuation of research on determining the effects of pre- and postweaning environment on feed efficiency. Previous research has established these time periods as critical periods of development (Gasser, 2013). However, little is known about how nutrient availability during these times affects feed utilization in later life.

The current study supports using various grazing and management strategies of developing replacement heifers common to Idaho with limited effects on indicators of reproductive success.

	Yea	r 1	Yea	ar 2	
Nutrient	Actual	DM	Actual	DM	Unit
Dry Matter	65.5	100	63.0	100	%
Invert Sugars	20.8	31.7	19.8	31.4	%
Crude Protein	13.3	20.3	12.6	20.0	%
CP as NPN	4.50	6.88	4.72	7.49	%
Crude Fat	0.99	1.52	0.77	1.23	%
Salt	5.94	9.07	5.94	9.43	%
Calcium	2.06	3.15	2.00	3.17	%
Phosphorus	1.00	1.53	1.00	1.59	%
Magnesium	0.22	0.34	0.20	0.32	%
Potassium	7.31	11.2	3.04	4.82	%
Sulfur	0.34	0.52	0.42	0.66	%
Iron	266	406	252	400	ppm
Manganese	442	674	440	699	ppm
Zinc	551	841	550	873	ppm
Copper	176	269	166	264	ppm
Cobalt	8.00	12.2	8.00	12.7	ppm
Iodine	51.7	78.9	51.7	82.0	ppm
Selenium	3.29	5.02	3.20	5.08	ppm
Vitamin A	34927	53321	34927	55439	IU/kg
Vitamin D	2451	3809	2495	3960	IU/kg
Vitamin E	440	672	440	699	IU/kg
Monensin	245	382	245	397	mg/kg
Net Energy Maintenance	1.08	1.65	1.08	1.72	Mcal/k
Net Energy Gain	0.75	1.14	0.75	1.17	Mcal/k

 Table 4.1. Nutrient composition of liquid supplement used during feed efficiency trial

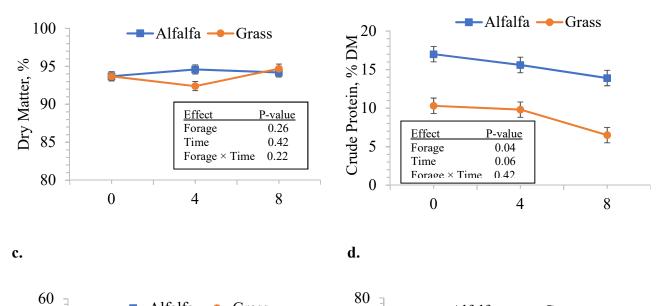
Table 4.2. Near-infrared spectroscopy analysis in yr 2 for preweaning treatment of heifers grazing either irrigated or range pastures with their dams.

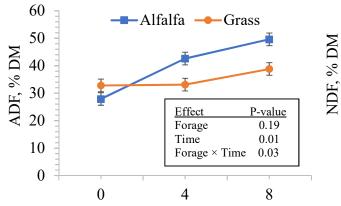
Mid-Summer		Weaning		<i>P</i> -value of Effect			
Nutrient Analysis	Irrigated	Range	Irrigated	Range	Location	Time	Location × Time
Crude Protein	$15.8\pm0.39^{\text{a}}$	15.9 ± 0.41^{a}	$16.2\pm0.44^{\rm a}$	12.1 ± 0.39^{b}	< 0.01	< 0.01	< 0.01
Digestible Organic Matter	$66.5\pm0.49^{\rm a}$	$65.2\pm0.52^{\rm a}$	68.8 ± 0.56^{b}	$61.1\pm0.49^{\text{c}}$	0.09	< 0.01	< 0.01

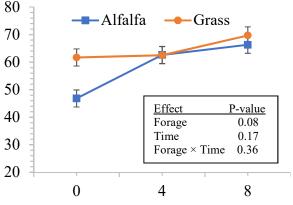
Samples were collected from 10 random heifers in mid-July and at weaning. Samples were analyzed remotely (D. R. Tolleson, Sonora A&M Agrilife Research Center, Sonora, TX and Grazingland Animal Nutrition Lab, Temple TX). Differing letters indicate a statistical difference (P < 0.05).

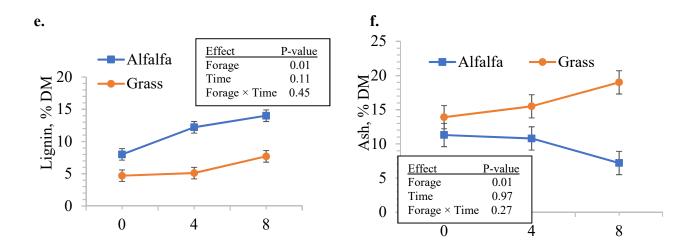
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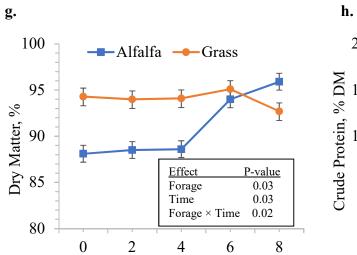


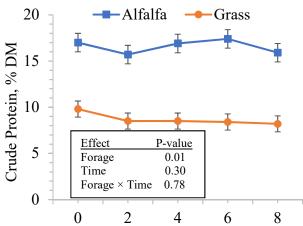


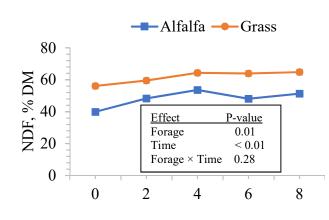


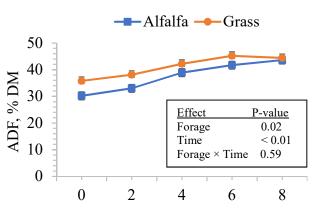










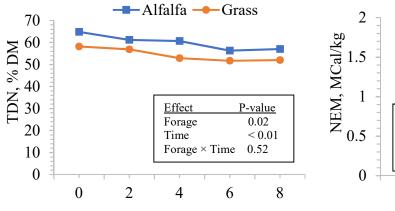


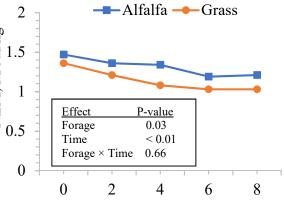
j.

l.



i.





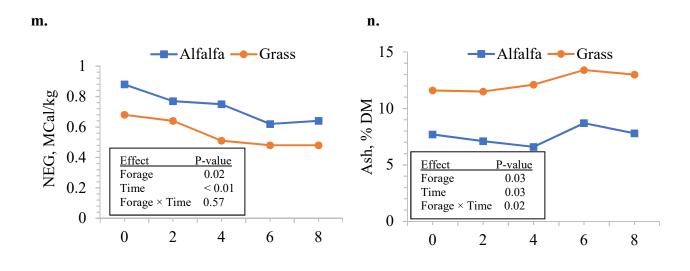


Figure 4.1a-n: Heifer diet quality as estimated by forage samples taken during postweaning grazing treatment. Diet quality was estimated by wet chemistry analysis of samples taken at various time points during a 2-month postweaning trial, during which heifers grazed either alfalfa or grass pastures. The trial was conducted over 2 years and years were analyzed separately using repeated measures in a mixed model. The y-axis is the variable of interest and the x-axis is the number of weeks from the start of the trial. Figure 4a-f are yr 1; 4g-n are yr 2. In yr 1, forage analysis was performed at UI. In yr 2, forage analysis was sent for remote analysis (Cumberland Valley Analytical Services, Inc., Waynesboro, PA).

Table 4.3. Effect of preweaning treatment on growth and reproductive traits in beef heifers grazing irrigated or rangeland pastures before weaning. Heifers grazed with dams on either irrigated pastures in Salmon, ID or on rangeland pastures in Hailey, ID from 3 mo of age to weaning.

Item	Irrigated	Range	SEM	<i>P</i> -value
Weaning wt, kg	265.9	251.8	± 3.7	0.13
ADG, birth to weaning, kg/d	1.1	1.0	± 0.02	0.10
Postweaning treatment end wt, kg	299.4	281.4	± 5.8	0.03
Postweaning ADG, kg/d	0.21	0.33	± 0.05	0.08
Wt at ultrasound, kg	390.0	377.0	± 4.3	0.12
Antral follicle count	14.1	14.5	± 1.5	0.76
Reproductive tract score	3.6	3.5	± 0.1	0.69
Pubertal, %	49.3	44.1	-	-
AI pregnancy rate, %	60.3	53.0	± 0.3	0.43
Final pregnancy rate, %	89.7	91.0	± 0.6	0.81

¹ Antral follicle count and reproductive tract score were determined for heifers 10 d before beginning 14-d CIDR synchronization protocol. In yr 1, pubertal status was determined by 2 serum progesterone samples taken at d -10 and d 0 before CIDR insertion but was not analyzed statistically due to lack of replication. Pregnancy rate to AI was determined by PSPB blood samples and ultrasound. Bold font indicates statistical tendency ($0.05 > P \le 0.10$) or difference ($P \le 0.05$).

Table 4.4. Effect of postweaning treatment on growth and reproductive traits in beef heifers grazing alfalfa or grass pastures for 2 mo after weaning. One month after weaning, heifers grazed either alfalfa or grass pastures for 2 months and were then comingled and treated similarly through the breeding season.

Item	Alfalfa	Grass	SEM	<i>P</i> -value
Postweaning treatment beginning wt, kg	272.2	277.1	± 5.0	0.52
Postweaning treatment end wt, kg	294.2	286.7	± 5.8	0.22
Postweaning ADG, kg/d	0.38	0.17	$\pm \ 0.05$	0.02
Wt at ultrasound, kg	388.8	378.1	± 4.3	0.18
Antral follicle count ¹	14.9	13.7	± 1.5	0.31
Reproductive tract score ¹	3.6	3.5	± 0.1	0.55
Pubertal ¹ , %	47.8	45.6	± 0.1	0.79
AI pregnancy rate ¹ , %	59.9	53.1	± 0.3	0.46
Final pregnancy rate, %	91.2	89.4	± 0.6	0.71

¹ Antral follicle count and reproductive tract score were determined for heifers 10 d before beginning 14-d CIDR synchronization protocol. In yr 1, pubertal status was determined by 2 serum progesterone samples taken at d -10 and d 0 before CIDR insertion. Pregnancy rate to AI was determined by PSPB blood samples and ultrasound. Bold font indicates statistical tendency ($0.05 > P \le 0.10$) or difference ($P \le 0.05$).

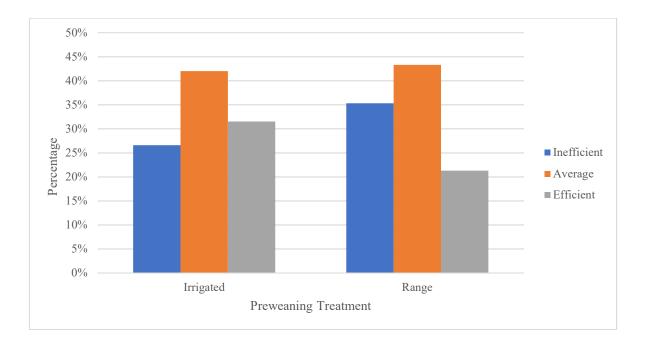


Figure 4.2. Influence of preweaning grazing treatment on proportion of heifers in different residual feed intake groups. Heifers were grazed with dams on either irrigated pastures or on rangeland in Idaho. While not significant (P = 0.1), the patterns of heifers classified as inefficient, average or efficient across irrigated and range treatments indicate some differences where the proportion of efficient heifers in the irrigated treatment was larger than that of the range treatment.

CHAPTER 5: RELATIONSHIP BETWEEN FEED EFFICIENCY AND FERTILITY IN BEEF HEIFERS

ABSTRACT

The objective of this study was to determine the relationship between residual feed intake (RFI) and fertility in beef heifers. Crossbred Angus, Hereford and SimAngus sired heifers (n = 293) were fed for a 70-d feed trial in a GrowSafe system to determine RFI and then grouped as inefficient, average, and efficient within year. Heifers were weighed every 2 wk. Heifers averaged 336.8 ± 1.0 d of age, 316.2 ± 1.9 kg at the initiation of the feed trial and 413.1 ± 2.1 kg at the end of the trial. On d 48 and d 55 of the RFI trial in yr 1 and yr 2 respectively, reproductive tract scores (RTS) and antral follicle counts (AFC) were determined via ultrasound. In yr 1, blood samples for progesterone analysis were obtained at the same time and 10 d later when heifers were estrous synchronized using the 14 Day CIDR Split-Time AI protocol. Heifers with at least 1 progesterone sample > 1.0 ng/mL were considered cyclic. Pregnancy was determined by ultrasound on d 42, 60 and 142 after AI. Chi-square analysis was used to evaluate differences in proportions in RTS, AFC, pubertal status at the beginning of synchronization, and PR among RFI classifications. Reproductive tract score was not different (P = 0.18) among RFI classifications. Furthermore, there was no difference among cyclic heifers in the inefficient group compared to the efficient group (RTS score of 4 or 5; P = 0.81). Pubertal status as measured by progesterone levels before synchronization was similar for inefficient, average, and efficient groups (52%, 45%, 43%, respectively). Antral follicle count category was not different (P = 0.13) among RFI groups. Similarly, AI PR and final PR were not different (P = 0.80, P = 0.74, respectively) between RFI groups, averaging 57.3% and 90.0%, respectively. In conclusion, reproductive development as measured by RTS, AFC, pubertal status, and PR was not different were not different between RFI groups. Beef producers may be able to select for RFI with limited impact on fertility. However, the results from this study indicate continued research with large datasets on RFI and fertility in beef heifers is warranted.

INTRODUCTION

The cow/calf industry is an important part of the United States economy, representing the number one source of cash receipts in 2015 (USDA, 2016). Feed is the largest input cost to beef producers (Hall, 2013) and can vary greatly from year to year. Although much research and progress has been done to reduce the amount of input needed to maintain a profitable herd, improving efficiency of inputs used is another strategy to boost profits (Arthur and Herd, 2008). Various methods have been used to select for more efficient cattle that differ in labor, costs, and measurements needed. Measuring residual feed intake is a common method and is independent from measures such as ADG and BW (Arthur and Herd, 2008); therefore, RFI is a more accurate representation of the efficiency of metabolic processes within the animal (Herd and Arthur, 2009).

Reproductive failure characterizes another major cost to the beef industry (Hall, 2013). However, selecting for reproductive efficiency is challenging, as measurements such as pregnancy rate and age at first calving are lowly heritable (Cushman and Perry, 2012). This is mostly due to many potential outside factors. Other measurements, such as RTS and AFC, although more difficult to assess, are moderately heritable and reflect an individual's potential fertility (Cushman and Perry, 2012), therefore eliminating many environmental factors that affect attainment of pregnancy.

Reproductive tract scores are performed by palpation and/or ultrasound in heifers before the breeding season and denote sexual maturity (LeFever and Odde, 1986). Scores of 1 to 5 semi-objectively classify heifers into groups of prepubertal, peripubertal and pubertal animals based on ovarian structures and size and tone of the tract. Performing RTS can assist in management decisions, such as nutritional regiments and synchronization protocols (Martin et al., 1992; Kasimanickam et al., 2016). Heifers with a greater RTS are more likely to become pregnant and achieve pregnancy earlier in the breeding season (Gutierrez et al., 2014).

Antral follicle counts are performed by ultrasound and appear to be an acceptable measure of an individual's inherent fertility (Ireland et al., 2008; Cushman et al, 2009; Jimenez-Krassel et al., 2015). Heifers are determined to have a low, medium or high AFC based on the number of follicles \geq 3 mm. Heifers classified as high have increased PR

(Cushman et al., 2009) and longer reproductive lifespans (McNeel and Cushman, 2015; Jimenez-Krassel et al., 2015).

Reproductive efficiency and RFI are both moderately heritable traits (Arthur and Herd, 2008; Cushman and Perry, 2012), which can enable producers to effectively select for these traits when choosing replacement heifers. However, there is evidence these traits may not be independent, and heavy selection pressures for one trait may consequently affect the other trait. Basarab and colleagues (2011) and Shaffer and colleagues (2011) noted earlier maturing heifers were less efficient than later maturing heifers. Although pubertal attainment in efficient heifers only occurred 7 to 11 d later than inefficient heifers in these studies, Basarab and colleagues noted lower PR as well. Although some research has been done investigating the relationship between feed efficiency and sexual maturity (reviewed by Randel and Welsh, Jr., 2013), limited research has been focused on interactions between feed efficiency and inherent fertility.

OBJECTIVES AND HYPOTHESES

The first objective of this study was to investigate the differences in RTS, AFC, pubertal status at synchronization, and PR among RFI groups. The null hypothesis was that the proportion of heifers in various RTS and AFC categories, and the proportion of heifers achieving puberty and pregnancy, would not differ among RFI groups. The second objective was to examine the relationship between fertility, as measured by RTS and AFC, and individual components of determining RFI. The null hypothesis was that no relationship would be evident between these traits.

MATERIALS AND METHODS

All procedures were approved by the UI IACUC protocol numbers #2016-56 and #2015-19.

Feed efficiency trial

Crossbred heifers were used in a feed efficiency trials replicated over 2 years (yr 1: n = 139; age = 342.3 ± 1.4 ; start BW = $320.7 \text{ kg} \pm 2.9$; end BW = 414.7 ± 3.0 ; yr 2: n = 154;

age = 331.9 ± 1.2 ; start BW = $312.5 \text{ kg} \pm 2.4$; end BW = 412.1 ± 2.9) were placed into 4 pens each equipped with 5 feeding nodes (GrowSafe, Calgary, Alberta, Canada) at NMCREEC. Heifers were sired by Angus (n = 88), Hereford (n = 51), SimAngus (n = 138)or other beef bulls (n = 16). Descriptive statistics are presented in Table 5.3. Pen assignment was by body weight to ensure heifers were in a pen with contemporaries of a similar body weight. Residual feed intake was determined over a 77 d and 85 d period in yr 1 and 2, respectively. Heifers were weighed over 2 consecutive days at the initiation and conclusion of the trial and every 2 wk during the study. Ultrasound backfat was determined at the conclusion of the trial and used in RFI calculations. Heifers were fed a diet of 80% alfalfa hay, 10% wheat middlings, and 10% liquid supplement (PerforMix Nutrition, Nampa, ID; Table 5.1). All diets were prepared daily as a total mixed ration and fed *ad libitum*. Daily feed samples were collected and dried to obtain DM percentage. This was used to determine daily DMI for feed efficiency calculation. Daily feed samples were composited into 2 time periods and components analyzed (Cumberland Valley Analytical Services, Inc., Waynesboro, PA) to give an estimate of diet quality. Nutrient analysis of heifer diets for yr 1 and 2 are provided in Table 5.2.

Reproductive data and estrous synchronization

Reproductive data collection and synchronization was collected and performed as in Chapter 4.

Statistical analysis

To determine RFI, actual individual daily DMI was regressed against predicted intake based on ADG during the feeding period, using metabolic bodyweight at midpoint and ultrasound ribfat as adjustments. Heifers were ranked by RFI and classified as inefficient, average, or efficient based on the number of standard deviations from the mean of all heifers in the study (> 0.5 SD above mean, \pm 0.5 within SD, and < 0.5 SD, respectively).

In yr 1, the following equation was used:

$$RFI = DMI - [-1.00079 + (0.13194 \times MBW) + (2.37991 \times ADG) + (0.05426 \times RIBFT)]$$

In yr 2, the following equation was used:

$$RFI = DMI - [0.24519 + (0.11884 \times MBW) + (0.87450 \times ADG) + (0.04555 \times RIBFT)]$$

Chi-square analysis using SAS Proc FREQ was used to test for differences in proportions of heifers in different RTS and AFC classifications, pubertal status, AI and final PR among inefficient, average, and efficient heifers. Sire breed distribution was evaluated among RFI groups after removing 16 animals not sired by Angus, Hereford, or SimAngus bulls.

For further investigation, RTS categories were collapsed to prepubertal (1 to 3 score) or pubertal (4 or 5 score) and compared between heifers ranked as inefficient or efficient (heifers ranked as average were removed from the dataset) and were compared by using a Chi-square analysis (SAS Proc FREQ).

A log transformation was performed on AFC to investigate the relationship between RFI value and AFC using Proc MIXED. Using Proc GLM, the effect of RFI equation variables (ADG, DMI, MBW, and RIBFT) and body weight at the time of ultrasounding (USWT) on AFC and RTS was tested. For all analyses, significance was declared at $P \le 0.05$ and a statistical tendency declared at P > 0.05 and $P \le 0.10$.

RESULTS

Heifers were ranked as inefficient (yr 1: n = 44; yr 2: n = 47), average (yr 1: n = 55; yr 2: n = 70;) and efficient (yr 1: n = 40; yr 2: n = 37). Sire breed was different among RFI groups, with a greater percentage of SimAngus sired heifers ranking as inefficient or average compared to Angus and Hereford sired heifers (P < 0.01; Fig. 5.1).

Reproductive development and fertility measures among RFI groups are presented in Fig. 5.2 and 5.3 and Table 5.4. There was no difference in pubertal status in yr 1 among inefficient, average or efficient heifers (P = 0.65, yr 1, Table 5.4), or among RTS ($\leq 2-5$) classifications (P = 0.18; data not shown). When RTS categories were collapsed for further analysis, there was no difference (P = 0.82) among inefficient and efficient groups (Fig. 5.2). There was no difference in the proportion of heifers in low, medium or high AFC

categories among RFI classifications (P = 0.21, Fig. 5.3). Pregnancy rate among heifers to AI (P = 0.80) and final PR (P = 0.74) was also not different among RFI classifications (Table 5.4).

Antral follicle count was negatively related to ADG (P = 0.02; $r^2 = 0.03$, Fig. 5.4a) and positively related to DMI (P = 0.04; $r^2 = 0.02$, Fig. 5.4b) during the RFI trial. Ribfat, MBW and USWT were not related to AFC (P = 0.43, P = 0.53, P = 0.48, respectively).

Reproductive tract score was not related to ADG (P = 0.91), however tended to be positively related to both DMI (P = 0.06; $r^2 = 0.01$, Fig. 5.5a) and ribfat (P = 0.08; $r^2 = 0.01$, Fig. 5.5b) and was positively related to MBW and USWT (P < 0.01; $r^2 = 0.10$ and P < 0.01; $r^2 = 0.09$, respectively, Fig. 5.5c and 5.5d). There was no relationship detected between RFI value and log AFC (P = 0.78).

DISCUSSION

Feed efficiency is an important selection trait when choosing replacement heifers to maximize profit. However, because feed efficiency is problematic to measure on a large scale, it is difficult to determine if selection pressure for feed efficiency may negatively influence other traits. Therefore, the purpose of this study was to investigate differences in reproductive traits among heifers in different RFI categories.

Sire breed differences were detected among RFI categories. Breed differences in RFI have been demonstrated in other studies as well (Crowley, et al., 2010; Retallick et al., 2017), however, in those studies, Angus were less efficient than continental breeds and Herefords. In contrast, in the current study, Angus and Hereford sires had more heifers ranked as efficient than SimAngus sires. However, the purpose of this study was not to quantify breed differences and it should be considered that a low number of sires in each breed were used to sire heifers.

Reproductive measures and feed efficiency

In the current study, reproductive measures including AFC, RTS, pubertal status, and PR were not different among RFI classifications. This indicates selection for efficient replacement heifers, or culling inefficient heifers, may not impact herd reproductive success.

Reproductive measures and components of RFI

Antral follicle count may be used as a measure of fertility and is indicative of reproductive success and age at first calving (Ireland et al., 2008; McNeel and Cushman, 2015). The number of follicles present on the ovary \geq 3 mm is indicative of the ovarian reserve and the female's lifetime supply of primordial follicles (Ireland et al., 2008). Additionally, AFC can be accurately represented by serum anti-Müllerian hormone (AMH) levels, which may be an inexpensive, practical measure for producers to predict fertility in the future (Rico et al., 2009; Jimenez-Krassel et al., 2015). Antral follicle count was negatively related to ADG and was positively related to DMI. This suggests inefficient heifers may have a greater AFC, however, there was no difference in the number of high or low AFC animals between RFI groups. The relationship between AFC and ADG in this study conflicts previous research (Eborn et al., 2013) in which ADG was positively correlated with AFC. However, Eborn and colleagues examined heifers from 8 to 15 mo of age, whereas the current study focused on heifers from 11 to 13.5 mo and on an *ad libitum* diet. These conflicting results supports further research to better understand this relationship.

Reproductive tract scoring is a practical, inexpensive way for producers to determine pubertal status using size and tone of the tract and structures on the ovaries (LeFever and Odde, 1986). Pregnancy rate and longevity are improved in heifers with a greater RTS (Holm et al., 2016). Dry matter intake, and RIBFT tended to be positively related to RTS, while MBW and USBW were positively related to RTS.

Reproductive tract score has been determined to be positively affected by weight, as well as BCS, which is a visual appraisal of body fat (Hall, 2005; Holm et al., 2009). Multiple studies have demonstrated inefficient animals are fatter, hence this trait is often used as an adjustment factor in calculating RFI (Basarab et al., 2003; Basarab et al., 2009). However, even when using backfat as an adjustment, efficient heifers still achieved puberty 11 d after inefficient heifers (Basarab et al., 2011).

In the current study, a tendency for a relationship between RTS and DMI was detected, which may have been due to heavier heifers having increased intake. However, DMI largely contributes to individual differences in RFI and feed efficiency (Basarab et al., 2003; Arthur and Herd, 2008), and efficient animals consume less feed. Basarab and colleagues (2011) demonstrated pubertal status affects intake and feed efficiency. Pubertal heifers ate 4.7% more feed than pre-pubertal heifers and were 7.4% less efficient when using feed conversion ratio calculation (Basarab et al., 2011). This was hypothesized to be partially due to both increased activity associated with estrus and increased fat composition (Basarab et al., 2009, Basarab et al., 2011, Shaffer et al., 2011; Basarab et al., 2012). Additionally, Loyd and colleagues (2011) reported a moderate correlation (r = 0.48) between pre-pubertal and pubertal RFI ranking, indicating metabolic processes change with achievement of puberty and there is variation in these changes among individuals. Despite these relationships between RTS and the components of determining RFI, RTS was not different among RFI groups.

Other studies have shown a negative relationship between feed efficiency and age at puberty determined by measuring serum progesterone every 7 to 11 days (Basarab et al., 2011; Shaffer et al., 2011). Reproductive tract scoring is a semi-objective, quantitative way to estimate reproductive maturity of heifers at one point in time, which, due to its nature, limits the power to detect statistical differences. These discrepancies support the value of additional research to further understand the relationship between RFI and reproductive development. If differences do exist, the severity of the impact on PR would also need to be determined.

Pregnancy rate was not related to RFI in the current study, however, previous studies reported a 9.5% lower PR in efficient heifers (Basarab et al., 2011) and a 5 to 6 d delay in pregnancy in cows producing more efficient progeny (Basarab et al., 2007). Pregnancy rate can be influenced by many factors, including BCS (Morrison, et al. 1999; Hess et al., 2005), and RTS at synchronization (Gutierrez et al., 2014).

The present study detected relationships between RFI components and AFC and RTS. However, no differences were seen between RFI categories for these traits. This could be due to several reasons. First, RFI is a better measure of efficiency than individual components of RFI, such as ADG and DMI (Arthur and Herd, 2008), and efficiency is not directly linked to reproduction. Second, it is more challenging to achieve statistical power when using categorical data compared to qualitative data. This is further compounded by the relatively low number of animals within a feed efficiency group and AFC group or RFI score.

Determining individual feed efficiency is expensive and time-consuming, whereas traits such as ADG and BW are easy for producers to determine. However, selecting solely for these traits may result in larger frame sizes and decreased efficiency (Arthur and Herd, 2008). The current study suggests that selecting for traits such as ADG, BW and fatness may also influence reproductive success. The relationship between feed efficiency and reproductive traits should continue to be investigated with a larger number of animals and across multiple herds. Many genes regulating muscle development, feed efficiency, and reproductive development are similar (Cánovas et al., 2014). These results also support the need for robust research to further validate genetic markers and other inexpensive ways to improve selection for feed efficiency. This would enable producers to select for feed efficiency rather than BW and ADG; therefore, potentially decreasing selection pressure on reproductive development.

Conclusions

This study detected no differences in AFC or RTS among heifers in different RFI groups. It is possible producers may be able to select efficient heifers without impacting reproductive success. Both AFC and RTS are practical screening methods to incorporate into replacement heifer selection programs if individuals are trained. Therefore, these measures, along with accurate SNP tests for feed efficiency may allow producers to select the most profitable animals in the future.

	Yea	r 1	Yea	Year 2	
Nutrient	Actual	DM	Actual	DM	Unit
Dry Matter	65.5	100	63.0	100	%
Invert Sugars	20.8	31.7	19.8	31.4	%
Crude Protein	13.3	20.3	12.6	20.0	%
CP as NPN	4.50	6.88	4.72	7.49	%
Crude Fat	0.99	1.52	0.77	1.23	%
Salt	5.94	9.07	5.94	9.43	%
Calcium	2.06	3.15	2.00	3.17	%
Phosphorus	1.00	1.53	1.00	1.59	%
Magnesium	0.22	0.34	0.20	0.32	%
Potassium	7.31	11.2	3.04	4.82	%
Sulfur	0.34	0.52	0.42	0.66	%
Iron	266	406	252	400	ppm
Manganese	442	674	440	699	ppm
Zinc	551	841	550	873	ppm
Copper	176	269	166	264	ppm
Cobalt	8.00	12.2	8.00	12.7	ppm
Iodine	51.7	78.9	51.7	82.0	ppm
Selenium	3.29	5.02	3.20	5.08	ppm
Vitamin A	34927	53321	34927	55439	IU/kg
Vitamin D	2451	3809	2495	3960	IU/kg
Vitamin E	440	672	440	699	IU/kg
Monensin	245	382	245	397	mg/kg
Net Energy Maintenance	1.08	1.65	1.08	1.72	Mcal/k
Net Energy Gain	0.75	1.14	0.75	1.17	Mcal/k

RESULTS: TABLES AND FIGURES

Table 5.1. Nutrient analysis of vitamin and mineral supplement fed to heifers during feed efficiency trial in yr 1 and 2.

	Year	1	Year 2		
-	Period ²		Period ²		
Item	1	2	1	2	
Diet, % Dry matter	87.3	87.5	87.7	87.5	
Nutrient Analysis					
Crude protein ¹	15.3	13.6	13.3	13.7	
Acid detergent fiber ¹	39.9	44.6	45.8	45.2	
Neutral detergent diber ¹	48.4	54.5	55.2	57.1	
Total digestible nutrients ¹	55.1	56.3	56.7	56.6	
Net energy maintenance, Mcal/kg	1.14	1.19	1.19	1.19	
Net energy gain, Mcal/kg	0.57	0.62	0.64	0.64	

Table 5.2. Nutrient composition of the diet fed to heifers during a residual feed intake (RFI) trial in yr 1 and 2.^{1,2}

¹ Values reported on a dry matter basis ² Period 1: yr 1: 1/25/17 to 3/11/1; yr 2: 1/16/18 to 3/01/18. Period 2: yr 1: 3/12/17 to

4/12/17; yr 2: 3/02/18 to 4/12/17.

Table 5.3. Descriptive statistics of heifers in a feed efficiency trial over 2 years.

Item	Mean	SEM	
п	293	-	
Age	336.8	0.96	
Start BW, kg	316.2	1.89	
End BW, kg	413.1	2.08	
ADG, kg/d	1.2	0.01	
DMI, kg/d	12.4	0.09	
Ribfat, cm	4.5	0.07	

Item	Inefficient	Average	Efficient	Chi-Square
Pubertal status ¹ , yr 1, %	52.3	45.5	42.5	0.65
AI pregnancy rate ² , %	56.2	59.2	56.6	0.8
Final pregnancy rate ² , %	88.4	90.9	90.5	0.74

Table 5.4. Pubertal and pregnancy rates of heifers of differing residual feed intake classifications.^{1,2}

¹ In yr 1, pubertal status at the beginning of synchronization was determined by serum progesterone levels by RIA, with blood samples taken 10 d before and at CIDR insertion. ² Pregnancy rate was determined by ultrasound at 42 and 64 d and by palpation at 142 d.



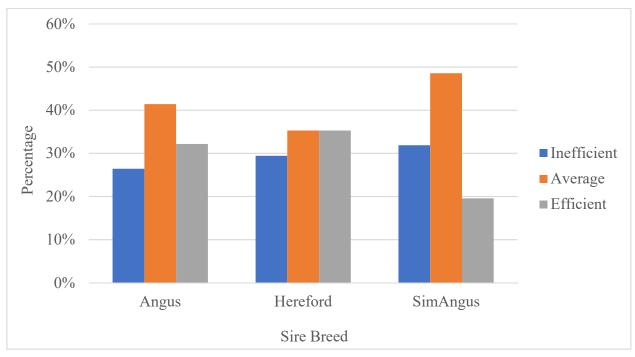


Figure 5.1. Residual feed intake (RFI) classifications among sire breeds. Heifers from different sire breeds were used in an RFI trial. The statistical differences observed (P < 0.01) in feed efficiency among progeny from different sires indicate heifers sired by Angus and Hereford sires used in the study were more likely to rank as average or efficient RFI.



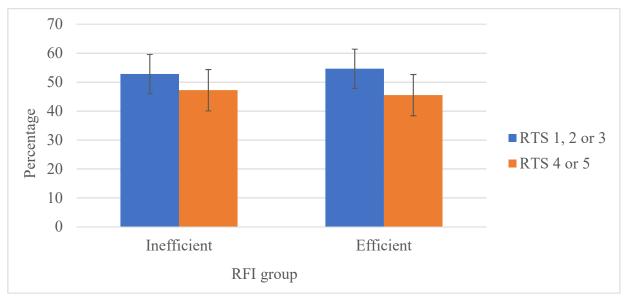


Figure 5.2. Reproductive tract scores (RTS) of heifers in different residual feed intake (RFI) groups. Heifers were assigned RTS at the start of synchronization. There was no difference in the occurrence of RTS \leq 3 and RTS \geq 4 (*P* = 0.82).

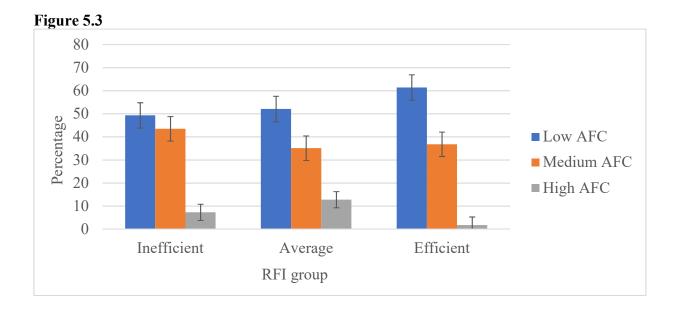


Figure 5.3. Antral follicle count (AFC) of heifers in different residual feed intake (RFI) groups. Antral follicle count was determined at the start of synchronization. There was no difference (P = 0.21) in occurrence of heifers with low (≤ 15 follicles), medium (16 to 24 follicles), and high (≥ 25 follicles) AFC in different RFI groups.



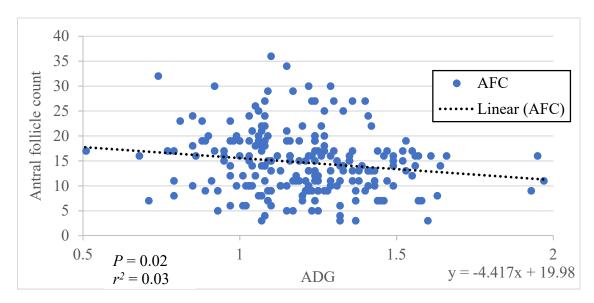


Figure 5.4b.

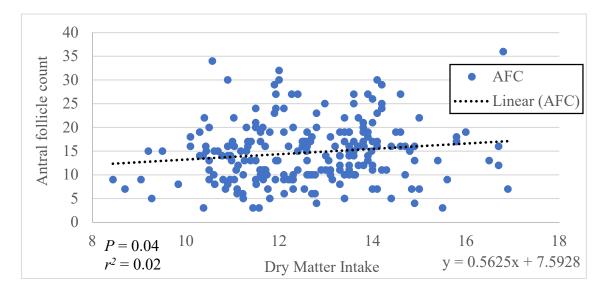


Figure 5.4. Relationship between antral follicle count (AFC) and average daily gain (ADG, 5.4a) and dry matter intake (DMI, 5.4b) during a residual feed intake (RFI) trial. Heifers on an RFI trial were evaluated 10 d before synchronization for AFC. There was a negative relationship between AFC and ADG (P = 0.02). In contrast, there was a positive relationship between AFC and DMI (P = 0.04).



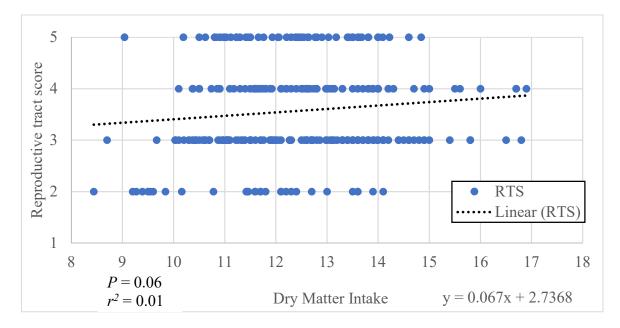


Figure 5.5b.

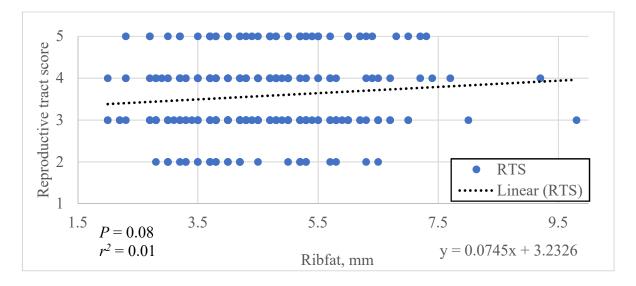


Figure 5.5c.

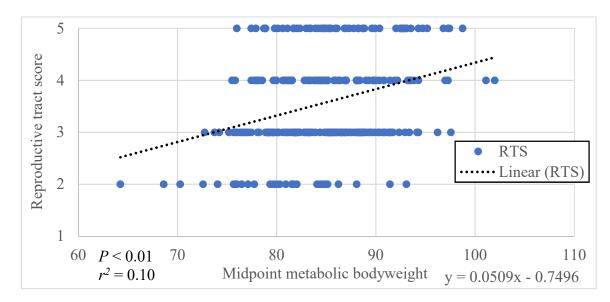
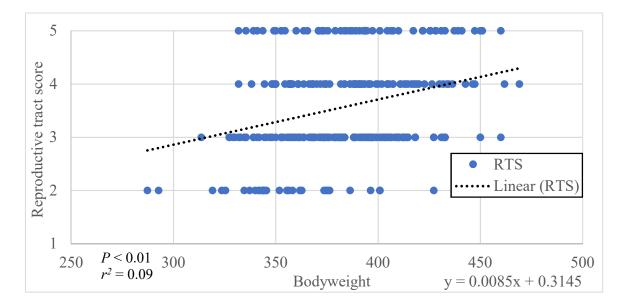
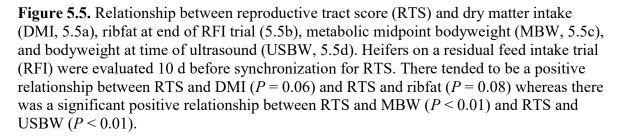


Figure 5.5d.





CHAPTER 6: CONCLUSIONS

The research discussed here builds on current knowledge and aids in further understanding the implications of management decisions when developing replacement beef heifers. These studies also provide a basis for further research of heifer development.

Preceding research has established the importance of proper nutrition to reproductive development. Rigorous studies across various environments have also established timing of nutrition and growth may be manipulated for economic advantages without impairing reproductive performance, provided heifers reach sexual maturity before the breeding season. The current research supports the economic viability of managing heifers in differing preweaning and postweaning environments. No treatment effects on two reproductive traits (RTS and AFC) were detected. These traits are indicative of future reproductive success and are reasonable for some producers to use when selecting replacement heifers. Future research investigating the effects of preweaning and postweaning environment on lifetime performance and reproductive lifespan will aid in educating long-term management decisions made by producers.

Previous experimentation indicates developmental programming occurs in early life and affects lifetime performance of both steer and heifer calves. The discussed preliminary research investigating the effects of pre- and postweaning environment on yearling feed efficiency supports the need for further research. Continuing to rigorously study the effects of preweaning environment on lifetime efficiency will greatly benefit the beef industry. This research is necessary to further understand how to utilize land and feed resources, especially of land not suitable for farming, most efficiently while ensuring the sustainability of the beef industry.

There is considerable overlap in genes and metabolic pathways regulating growth and reproduction. Many of these genes are major players of metabolic regulation and development. Other studies have demonstrated an inverse relationship between sexual maturity and feed efficiency. The current data support evidence of a relationship between reproductive development and measures used to determine RFI. However, the magnitude of this association noted in previous studies and the current study supports selecting heifers for RFI, provided sexual maturity is considered. The current study also indicates fertility may be related to components used to determine RFI. Future research validating these results and further exploring the physiological relationship between RFI and reproduction would provide better information for selection decisions.

Further studies in these areas should focus on increased replication across various environments and multiple herds. This would allow for 1) validation of results from the current and previous studies, and 2) further dissemination of the information to beef producers. Also, studies using more quantitative measurements may increase knowledge of the discussed relationships and the physiological processes governing them. Additionally, continuing research investigating relationships between breed associations' genetic merit estimates of feed utilization and reproduction would be valuable. The combination of these methods allows for both the increased understanding of physiological processes, but also the impact of management decisions over a large scale and long time-period.

The current research utilized traits measurable by producers and indicative of a heifer's reproductive lifespan. The results of these studies aid in understanding how management practices common in Idaho and the Pacific Northwest affect herd productivity. Further research into physiological relationships will increase understanding of how to further manipulate these pathways in a way both sustainable and economical for beef producers.

REFERENCES

- Allen, C. C., L. O. Tedeschi, D. H. Keisler, R. C. Cardoso, B. R. C. Alves, M. Amstalden, and G. L. Williams. 2017. Interaction of dietary energy source and body weight gain during the juvenile period on metabolic endocrine status and age at puberty in beef heifers. J. Anim. Sci. 95:2080-2088. doi:10.2527/jas2016.1002
- Alves, B. R. C., R. C. Cardoso, L. D. Prezotto, J. F. Thorson, M. Bedenbaugh, S. M. Sharpton, A. Caraty, D. H. Keisler, L. O. Tedeshchi, G. L. Williams, and M. Amstalden. 2015. Elevated body weight gain during the juvenile period alters Neuropeptide Y-Gonadotropin-Releasing Hormone circuitry in prepubertal heifers. Biol. Reprod. 92:1-10. doi:10.1095/biolreprod.114.124636
- Amstalden, M., R. C. Cardoso, B. R. C. Alves, and G. L. Williams. 2014. REPRODUCTION SYMPOSIUM: Hypothalamic neuropeptides and the nutritional programming of puberty in heifers. J. Anim. Sci. 92:3211-3222. doi:10.2527/jas2014-7808
- Amundson, O. L., T. H. Fountain, E. L. Larimore, B. N. Richardson, A. K. McNeel, E. C. Wright, D. H. Keisler, R. A. Cushman, G. A. Perry, and H. C. Freetly. 2015.
 Postweaning nutritional programming of ovarian development in beef heifers. J. Anim. Sci. 93:5232- 5239. doi: 10.2527/jas.2015-9067.
- Arthur, J. P. F., and R. M. Herd. 2008. Residual feed intake in beef. R. Bras. Zootec. 37(Suppl.):269–279.
- Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189-204.
- Basarab, J. A., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87:489-502.
- Basarab, J. A., M. G. Colazo, D. J. Ambrose, S. Novak, D. McCartney, and V. S. Baron. 2011. Residual feed intake adjusted for backfat thickness and feeding frequency is independent of fertility in beef heifers. Can. J. Anim. Sci. 91.4 (2011): 573-584. doi:10.4141/cjas2011-010

- Basarab, J. A., C. Fitzsimmons, C. S. Whisnant, and R. P. Wettemann. 2012. Interactions with other traits: reproduction and fertility. In: R. A. Hill, editor, Feed efficiency in the beef industry. John Wiley & Sons, Inc., Ames, IA. p.123-144. doi:10.1002/9781118392331.ch9
- Burns, D. S., F. Jimenez-Krassel, J. L. H. Ireland, P. G. Knight, and J. J. Ireland. 2005.
 Numbers of antral follicles during follicular waves in cattle: evidence for high variation among animals, very high repeatability in individuals, and an inverse association with serum follicle-stimulating hormone concentrations. Biol. Reprod. 73:54-62. doi:10.1095/biolreprod.104.036277
- Buskirk, D. D., D. B. Faulker, and F. A. Ireland. 1995. Increased postweaning gain of beef heifers enhances fertility and milk production. J. Anim. Sci. 73:937-946.
- Cafe, L. M., D. W. Hennessy, H. Hearnshaw, S. G. Morris, and P. L. Greenwood. 2009. Consequences of prenatal and preweaning growth for feedlot growth, intake and efficiency of Piedmontese and Wagyu-sired cattle. Anim. Prod. Sci. 49:461–467. doi: 10.1071/EA08089
- Cánovas, A., A. Reverter, K. L. DeAtley, R. L. Ashley, M. L. Colgrave, M. R. S. Fortes, A. Islas-Trejo, S. Lehnert, L. Porto-Neto, G. Rincón, G. A. Silver, W. M. Snelling, J. F. Medrano, and M. G. Thomas. 2014. Multi-tissue omics analyses reveal molecular regulatory networks for puberty in composite beef cattle. PLoS ONE 9:e102551. doi:10.1371/journal.pone.0102551
- Cardoso, R. C., B. R. C. Alves, L. D. Prezotto, J. F. Thorson, L. O. Tedeschi, D. H. Keisler, C. S. Park, M. Amstalden, and G. L. Williams. 2014. Use of a stair-step compensatory gain nutritional regimen to program the onset of puberty in beef heifers. J. Anim. Sci. 92:2942-2949. doi:10.2527/jas2014-7713.
- Choat, W. T., C. R. Krehbiel, G. C. Duff, R. E. Kirksey, L. M. Lauriault, J. D. Rivera, B. M. Capitan, D. A. Walker, G. B. Donart, and C. L. Goad. 2003. Influence of grazing dormant native range or winter wheat pastures on subsequent finishing cattle performance, carcass characteristics, and ruminal metabolism. J. Anim. Sci. 81:3191-3201. doi: 10.2527/2003.81123191x
- Crews, D. H. 2005. Genetics of efficient feed utilization and national cattle evaluation: a review. Genet. Mol. Res. 4(2):152-165.

- Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885-894. doi:10.2527/jas.2009-1852
- Cushman, R. A., M. F. Allan, L. A. Kuehn, W. M. Snelling, A. S. Cupp, and H. C. Freetly.
 2009. Evaluation of antral follicle count and ovarian morphology in crossbred beef
 cows: Investigation of influence of stage of the estrous cycle, age, and birth weight.
 J. Anim. Sci. 87:1971–1980. doi:10.2527/jas.2008-1728
- Cushman, R. A. and G. A. Perry. 2012. What we know about the genetics of reproduction. Proc. Applied Reproductive Strageties, 165-174.
- Cushman, R. A., L. K. Kill, R. N. Funston, E. M. Mousel, and G. A. Perry. 2013. Heifer calving date positively influences calf weaning weights through six parturitions. J. Anim. Sci. 91:4486-4491. doi:10.2527/jas2013-6465
- Cushman, R. A., A. K. McNeel, and H. C. Freetly. 2014. The impact of cow nutrient status during the second and third trimesters on age at puberty, antral follicle count, and fertility of daughters. Livestock Sci. 162:252-258. doi:10.1016/j.livsci.2014.01.033
- Day, M. L., K. Imakawa, D. D. Zalesky, R. J. Kittok, and J. E. Kinder. 1986. Effects of restriction of dietary energy intake during the prepubertal period on secretion of luteinizing hormone and responsiveness of the pituitary to luteinizing hormonereleasing hormone in heifers. J. Anim. Sci. 62:1641-1648.
- Day, M. L. and L. H. Anderson. 1998. Current concepts on the control of puberty in cattle. J. Anim. Sci. 76(Suppl. 3):1-15.
- Drouillard, J. S. and G. L. Kuhl. 1999. Effects of previous grazing nutrition and management on feedlot performance of cattle. J. Anim. Sci. 77(Suppl. 2):136-146. doi:10.2527/1999.77suppl_2136x.
- Dickinson, R. E., L. Hryhorskyj, H. Tremewan, K. Hogg, A. A. Thomson, A. S. McNeilly, and W. C. Duncan. 2010. Involvement of the SLIT/ROBO pathway in follicle development in the fetal ovary. Reproduction. 139(2): 395-407. doi:10.1530/REP-09-0182

- Du, M., J. Tong, J. Zhao, K. R. Underwood, M. Zhu, S. P. Ford, and P. W. Nathanielsz. 2010. Fetal programming of skeletal muscle development in ruminant animals. J. Anim. Sci. 88:E51–E60. doi:10.2527/jas.2009-2311
- Durlinger, A. L. L., J. A. Visser, and A. P. N. Themmen. 2002. Regulation of ovarian function: the role of anti-Müllerian hormone. Reproduction. 124:601-609. doi: 10.1530/rep.0.1240601
- Eborn, D. R., R. A. Cushman, and S. E. Echternkamp. 2013. Effect of postweaning diet on ovarian development and fertility in replacement beef heifers. J. Amin. Sci. 91:4168-4179. doi:10.2527/jas2012-5877
- Echternkamp, S. E., A. J. Roberts, D. D. Lunstra, T. Wise, and L. J. Spicer. 2004. Ovarian follicular development in cattle selected for twin ovulations and births. J. Anim. Sci. 82:459-471. doi:10.2527/2004.822459x
- Erickson, B. H. 1966. Development and senescence of the postnatal bovine ovary. J. Anim. Sci. 25:800-805.
- Evans, A. C. O., G. P. Adams, and N. C. Rawlings. 1994. Endocrine and ovarian follicular changes leading up to the first ovulation in prepubertal heifers. J. Reprod. Fertil. 100:187-194.
- Evans, A. C. O., G. P. Adams, and N. C. Rawlings. 1994. Follicular and hormonal development in prepubertal heifers from 2 to 36 weeks of age. J. Reprod. Fertil. 102:463-470.
- Freetly, H. C., K. A. Vonnahme, A. K. McNeel, L. E. Camacho, O. L. Amundson, E. D. Forbes, C. A. Lents, and R. A. Cushman. 2014. The consequence of level of nutrition on heifer ovarian and mammary development. J. Anim. Sci. 92:5437–5443. doi:10.2527/jas2014-8086
- Funston, R. N., D. M. Larson, and K. A. Vonnahme. 2010. Effects of maternal nutrition on conceptus growth and offspring performance: Implications for beef cattle production. J. Anim. Sci. 88:E205–E215. doi:10.2527/jas.2009-2351
- Funston, R. N., J. L. Martin, D. M. Larson, and A. J. Roberts. 2012. Nutritional aspects of developing replacement heifers. J. Anim. Sci. 90:1166-1171. doi:10.2527/jas.2011-4569.

- Gasser, C. L., C. R. Burke, M. L. Mussard, E. J. Behlke, D. E. Grum, J. E. Kinder, and M. L. Day. 2006. Induction of precocious puberty in heifers II: Advanced ovarian follicular development. J. Anim. Sci. 84:2042–2049 doi:10.2527/jas.2005-637
- Gasser, C. L. 2013. Joint Alpharma-beef Species symposium: Considerations on puberty in replacement beef heifers. J. Anim. Sci. 91:1336–1340. doi:10.2527/jas.2012-6008
- Grings, E. E., T. W. Geary, R. E. Short, and M. D. MacNeil. 2007. Beef heifer development within three calving systems. J. Anim. Sci. 85:2048–2058 doi:10.2527/jas.2006-758
- Gutiérrez, C. G., J. Oldham, T. A. Bramley, J. G. Gong, B. K. Campbell, and R. Webb. 1997. The recruitment of ovarian follicles is enhanced by increased dietary intake in heifers. J. Anim. Sci. 1997:1876-1884.
- Gutierrez, K., R. Kasimanickam, A. Tibary, J. M. Gay, J. P. Kastelic, J. B. Hall, and W. D.
 Whittier. 2014. Effect of reproductive tract scoring on reproductive efficiency in beef heifers bred by timed insemination and natural service versus only natural service. Theriogenology. 81:918-924. doi:10.1016/j.theriogenology.2014.01.008
- Hall, J. B. 2005. Reproductive evaluation of heifers. Proc. Applied Repro. Strategies in Beef Cattle. Lexington, KY. 279-283
- Hall, J. B. 2013. Nutritional Development and the target weight debate. Vet. Clin. North. Am. Food. Anim. Pract. 29:537-554. doi:10.1016/j.cvfa.2013.07.015
- Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. J. Anim. Sci. 87(14, Suppl.):E64-E71. doi:10.2527./jas.2008-1345
- Hess, B. W., S. L. Lake, E. J. Scholljegerdes, T. R. Weston, V. Nayigihugu, J. D. C. Molle, and G. E. Moss. 2005. Nutritional controls of beef cow reproduction. J. Anim. Sci. 83(E. Suppl.):E90–E106
- Holm, D. E., P. N. Thompson, and P. C. Irons. 2009. The value of reproductive tract scoring as a predictor of fertility and production outcomes in beef heifers. J. Anim. Sci. 87:1934–1940. doi:10.2527/jas.2008-1579
- Honaramooz, A., J. Aravindakshan, R. K. Chandolia, A. P. Beard, P. M. Bartlewski, R. A. Pierson, N. C. Rawlings. 2004. Ultrasonographic evaluation of the pre-pubertal development of the reproductive tract in beef heifers. Anim. Reprod. Sci. 80:15-29. doi:10.1016/S0378-4320(03)00136-2

- Ireland, J. J., F. Ward, F. Jimenez-Krassel, J. L. H. Ireland, G. W. Smith, P. Lonergan, and A. C. O. Evans. 2007. Follicle numbers are highly repeatable within individual animals but are inversely correlated with FSH concentrations and the proportion of good-quality embryos after ovarian stimulation in cattle. Hum. Reprod. 22:1687-1695. doi:10.1093/humanrep/dem071
- Ireland, J. L. H., D. Scheetz, F. Jimenez-Krassel, A. P. N. Themmen, F. Ward, P. Lonergan, G. W. Smith, G. I. Perez, A. C. O. Evans, and J. J. Ireland. 2008. Antral follicle count reliably predicts number of morphologically healthy oocytes and follicles in ovaries of young adult cattle. Biol. Reprod. 79:1219–1225. doi:10.1095/biolreprod.108.071670
- Ireland, J. J., G. W. Smith, D. Scheetz, F. Jimenez-Krassel, J. K. Folger, J. L. H. Ireland, F. Mossa, P. Lonergan, and A. C. O. Evans. 2011. Does size matter in females? An overview of the impact of the high variation in the ovarian reserve on ovarian function and fertility, utility of anti-Müllerian hormone as a diagnostic marker for fertility and causes of variation in the ovarian reserve in cattle. Reprod. Fertil. Dev. 23:1-14.
- Jimenez-Krassel, F., J. K. Folger, J. L. Ireland, G. W. Smith, X. Hou, J. S. Davis, P. Lonergan, A. C. Evans, and J. J. Ireland. 2009. Evidence that high variation in ovarian reserves of healthy young adults has a negative impact on the corpus luteum and endometrium during estrous cycles in cattle. Biol.Reprod. 80:1272–1281. doi:10.1095/biolreprod.108.075093
- Jimenez-Krassel, F., D. M. Scheetz, L. M. Neuder, J. L. H. Ireland, J. R. Pursley, G. W.
 Smith, R. J. Tempelman, T. Ferris, W. E. Roudebush, F. Mossa, P. Lonergan, A. C.
 O. Evans, and J. J. Ireland. 2015. Concentration of anti-Müllerian hormone in dairy heifers is positively associated with productive herd life. J. Dairy Sci. 98:3036–3045. doi:10.3168/jds.2014-813
- Kasimanickam, R. K., W. D. Whittier, J. B. Hall, and J. P. Kastelic. 2016. Estrous synchronization strategies to optimize beef heifer reproductive performance after reproductive tract scoring. Theriogenology. 86:831-838. doi:10.1016/j.theriogenology.2016.03.004

- Kelly, A. K., M. McGee, D. H. Crews, Jr., A. G. Fahey, A. R. Wylie, and D. E. Kenny. 2010. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables and body composition traits in growing beef heifers. J. Anim. Sci. 88(1):109-123. doi:10.2527/jas.2009-2196
- LeFever, D. G. and K.G. Odde. 1986. Predicting reproductive performance in beef heifers by reproductive tract evaluation before breeding. CSU Beef Program Report Colorado State University, Fort Collins. pp. 13-15
- Leitman, N. R., D. C. Busch, J. F. Bader, D. A. Mallory, D. J. Wilson, M. C. Lucy, M. R. Ellersieck, M. F. Smith, and D. J. Patterson. 2008. Comparison of protocols to synchronize estrus and ovulation in estrous-cycling and prepubertal beef heifers. J. Anim. Sci. 86:1808–1818. doi:10.2527/jas.2008-0970
- Loyd, A. N., C. R. Long, A. W. Lewis, R. D. Randel. 2011. Effects of physiological age on residual feed intake of growing heifers. Open J. Anim. Sci. 1:89-92. doi:10.4236/ojas.2011.13011
- Martin, L. C., J. S. Brinks, R. M. Bourdon, and L. V. Cundiff. 1992. Genetic effects on beef heifer puberty and subsequent reproduction. J. Amin. Sci. 70:4006-4017.
- McNeel, A. K., R. A. Cushman. 2015. Influence of puberty and antral follicle count on calving day in crossbred beef heifers. Theriogenology. 84:1061-1066. doi:10.1016/j.theriogenology.2015.06.010
- Monniaux, D., L. Drouilhet, C. Rico, A. Estienne, P. Jarrier, J. Touzé, J. Sapa, F. Phocas, J. Dupont, R. Dalbiés-Tran, and S. Fabre. 2013. Regulation of anti-Müllerian hormone production in domestic animals. Reprod. Fertil. Dev. 25:1-16. doi: 10.1071/RD12270
- Monniaux, D., F. Clément, R. Dalbiés-Tran, A. Estienne, S. Fabre, C. Mansanet, and P. Monget. 2014. The ovarian reserve of primordial follicles and the dynamic reserve of antral growing follicles: What is the link? Biol. Repro. 90(4):85, 1-11. doi:10.1095/biolreprod.113.117077
- Morrison, D. G., J. C. Spitzer, and J. L. Perkins. 1999. Influence of prepartum body condition score change on reproduction in multiparous beef cattle calving in moderate body condition. J. Anim. Sci. 77:1048-1054. doi:10.2527/1999.7751048x

- Mossa, F., F. Jimenez-Krassel, J. K. Folger, J. L. Ireland, G. Smith, P. Lonergan, A. C. O. Evans, and J. J. Ireland. 2010. Evidence that high variation in antral follicle count during follicular waves is linked to alterations in ovarian androgen production in cattle. Reproduction 140:713–720. doi:10.1530/REP-10-0214
- Mossa, F., F. Carter, S. W. Walsh, D. A. Kenny, G. W. Smith, J. L. H. Ireland, T. B.
 Hildebrandt, P. Lonergan, J. J. Ireland, and A. C. O. Evans. 2013. Maternal
 undernutrition in cows impairs ovarian and cardiovascular systems in their offspring.
 Biol. Reprod. 88:1-9. doi:10.1095/biolreprod.112.107235
- Perry, G. A. 2012. PHYSIOLOGY AND ENDOCRINOLOGY SYMPOSIUM: Harnessing basic knowledge of factors controlling puberty to improve synchronization of estrus and fertility in heifers. J. Anim. Sci. 90:1172–1182. doi:10.2527/jas.2011-4572.
- Perry, G. A. 2016. Factors affecting puberty in replacement beef heifers. Theriogenology. 86:373-378. doi:10.1016/j.theriogenology.2016.04.051
- Randel, R. D., and T. H. Welsh, Jr. 2013. JOINT ALPHARMA-BEEF SPECIES SYMPOSIUM: Interactions of feed efficiency with beef heifer reproductive development. J. Anim. Sci. 91:1323-1328. doi:10.2527/jas2012-5679
- Rawlings, N. C., A. C. O. Evans, A. Honaramooz, and P. M. Bartlewski. 2003. Antral follicle growth and endocrine changes in prepubertal cattle, sheep and goats. Anim. Reprod. Sci. 78:259-270. doi:10.1016/S0378-4320(03)00094-0
- Retallick, K. J., J. M. Bormann, R. L. Weaber, M. D. MacNeil, H. L. Bradford, H. C.
 Freetly, K. E. Hales, D. W. Moser, W. M. Snelling, R. M. Thallman, and L. A.
 Kuehn. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. J. Anim. Sci. 95:1444-1450. doi:10.2527/jas2016.1260
- Rico, C., S. Fabre, C. Médigue, N. Clemente, F. Clément, M. Bontoux, J. Touzé, M. Dupont, E. Briant, B. Rémy, J. Beckers, and D. Monniaux. 2009. Anti-Müllerian hormone is an endocrine marker of ovarian gonadotropin-responsive follicles and can help to predict superovulatory responses in the cow. Biol. Reprod. 80: 50–59. doi:10.1095/ BIOLREPROD.108.072157

- Rico, C., C. Médigue, S. Fabre, P. Jarrier, M. Bontoux, F. Clément, and D. Monniaux. 2010. Anti-Müllerian hormone production in the cow: a multiscale study at endocrine, ovarian, follicular and granulosa cell levels. Biol. Reprod. 84: 560-571. doi 10.1095/biolreprod.110.088187
- Roberts, A. J., T. W. Geary, E. E. Grings, R. C. Waterman, and M. D. MacNeil. 2009. Reproductive performance of heifers offered ad libitum or restricted access to feed for a one hundred forty-day period after weaning. J. Anim. Sci. 87:3043-3052. doi:10.2527/jas.2008-1476
- Robinson, D. L., L. M. Cafe, and P. L. Greenwood. 2013. MEAT SCIENCE AND MUSCLE BIOLOGY SYMPOSIUM: Developmental programming in cattle: Consequences for growth, efficiency, carcass, muscle, and beef quality characteristics. J. Anim. Sci. 91:1428-1442. doi:10.2527/jas2012-5799
- Rodríguez-Sánchez, J. A., Sanz A. Tamanini C., and Casasús I. 2015. Metabolic, endocrine, and reproductive responses of beef heifers submitted to different growth strategies during the lactation and rearing periods. J. Anim. Sci. 93(8): 3871-3885. doi:10.2527/jas2015-8994
- Romar, R., T. De Santis, P. Papillier, C. Perreau, A. Thélie, M. E. Dell'Aquila, P. Mermillod, and R. Dalbiés-Tran. 2011. Expression of maternal transcripts during bovine oocyte *in vitro* maturation is affected by donor age. Reprod. Dom. Anim. 46:e23-e30. doi:10.1111/j.1439-0531.2010.01617.x
- Roselle, L., K. Launchbaugh, T. Jones, L. Babcock, R. Ambrosek, A. Stebleton, T. Brewer,K. Sanders, J. Mink, and G. Hyde. 2009. Rangelands: An introduction to Idaho's wild open spaces. University of Idaho College of Natural Resources.
- Rosenkrans, K. S., and D. K. Hardin. 2002. Repeatability and accuracy of reproductive tract scoring to determine pubertal status in beef heifers. Theriogenology 59:1087-1092.
- Schillo, K. K., J. B. Hall, and S. M. Hileman. 1992. Effects of Nutrition and Season on the Onset of Puberty in the Beef Heifer. J. Anim. Sci. 70:3994-4005
- Senger, P. L. 2012. Pathways to pregnancy and parturition. 3rd ed. Current Conceptions, Inc., Redmond, OR.

- Shaffer, K. S., P. Turk, W. R. Wagner, and E. E. D. Felton. 2011. Residual feed intake, body composition, and fertility in yearling beef heifers. J. Anim. Sci. 89:1028–1034. doi:10.2527/jas.2010-3322
- Shewmaker, G. E., and M. G. Bohle. 2010. Pasture and grazing management in the northwest. University of Idaho Extension, Moscow, ID.
- Short, R. E., and R. A. Bellows. 1971. Relationships among weight gains, age at puberty and reproductive performance in heifers. J. Anim. Sci. 32:127-131.
- Springman, S. A., H. R. Nielson, T. L. Meyers, and R. N. Funston. 2017. Effect of postweaning heifer development system on average daily gain, pregnancy rates, and subsequent feed efficiency as a pregnant heifer. J. Anim. Sci. 95:5320–5326. doi:10.2527/jas2017.1987
- Tolleson, D. R., and D. W. Schafer. 2014. Application of fecal near-infrared spectroscopy and nutritional balance software to monitor diet quality and body condition in beef cows grazing Arizona rangeland. J. Anim. Sci. 92:349-358. doi:10.2527/jas2013-6631
- USDA. 2016. Overview of the United States cattle industry. NASS, Agricultural Statistics Board, USDA.
- USDA/ERS. 2018. Farm income and wealth statistics, cash receipts by commodity. USDA/ERS.
- Welch, C. M., J. K. Ahola, J. B. Hall, G. K. Murdoch, D. H. Crews Jr., L. C. Davis, M. E. Doumit, W. J. Price, L. D. Keenan, and R. A. Hill. 2012. Relationships among performance, residual feed intake, and product quality of progeny from Red Angus sires divergent for maintenance energy EPD. J. Anim. Sci. 90:5107–5117. doi:10.2527/jas2012-5184