RECIPROCAL DIFFERENCES IN F_2 AND F_3 NELLORE-ANGUS HALFBLOOD STEERS FOR GROWTH AND HEALTH TRAITS

A Thesis

by

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ABSTRACT

Nellore-Angus halfblood reciprocal F_2 and F_3 steers (n = 372) produced in the Texas A&M AgriLife Research McGregor Genomics project were evaluated for weight and growth through different stages of life, including after a standardized bovine viral diarrhea virus (BVDV) challenge. The F_2 steers were sired by F_1 Nellore-sired (NA) or Angus-sired (AN) bulls out of F_1 NA and AN dams (4 reciprocal calf types of ANAN, ANNA, NAAN, NANA, where the breed type of the bull is listed first). The F_3 steers resulted from F_2 NANA parents. There were no differences due to calf type for birth weight. From birth to weaning the F_3 steers gained between 0.10 and 0.13 kg less ($P < 0.05$) per d than the F_2 steers. The F_3 steers were lighter than all F_2 calf types at weaning, a year of age, through a 42-d health trial, and 15 mo of age. The NAAN steers were the heaviest ($P < 0.05$) calf type for weaning weight, yearling weight and weight at 15 mo. During the 42-d health and feeding trial, weights of F_2 steers out of AN dams were 7 to 10 kg heavier ($P < 0.05$) than F_2 steers out of NA dams. A similar pattern existed for ADG; ADG of the F_3 steers was not significantly different from F_2 steers out of NA dams. The F_2 steers out of AN dams also had higher ($P < 0.05$) monocyte counts than F_2 steers out of NA dams. Although monocyte count was not correlated to ADG during the 42-d health trial, it was lowly and positively correlated (r = 0.14, $P = 0.008$) with ADG from weaning to a year of age. Different patterns of relationship were present stages among the different calf types. For the NANA (r = -0.52, $P = 0.003$), F_3 (r = -

0.22, *P* = 0.003) and NAAN (r= -0.20, *P* = 0.003) steers there was a negative correlation of rectal temperature change and ADG from d 0 to 14 post challenge. Rectal temperature change post BVDV challenge was positively correlated with ADG from weaning to yearling weight for NANA (r = 0.62, *P* = 0.002) and ANNA (r = 0.28, *P* = 0.026) steers. Only ANAN steers had a relationship of preweaning ADG with rectal temperature change from BVDV challenge (r = 0.43, *P* = 0.046). In these cattle, the apparent trade-offs between growth and health responses appear inconsistent. The nature and interpretations of these reciprocal differences remain unclear and warrant additional research.

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INTRODUCTION

Reciprocal differences among birth weights in first generation *Bos indicus*-*Bos taurus* crosses have been widely reported. Based on these studies, *Bos* i*ndicus*-sired calves out of *Bos taurus* dams have 6 to 9 kg heavier birth weights than *Bos taurus*-sired calves out of *Bos indicus* dams. Additionally, bull calves out of *Bos indicus* sires and *Bos taurus* dams have been shown to be 5 to 7 kg heavier at birth than contemporary heifer calves out of the same type of mating (Roberson et al., 1986; Amen et al., 2007a; Dillon et al., 2015), while there has been little if any difference in birth weight shown between bull and heifers calves out of crosses involving *Bos taurus* sires and *Bos indicus* dams (Roberson et al., 1986; Amen et al., 2007a; Dillon et al., 2015). Within both *Bos taurus* and *Bos indicus* straightbred calves, bull calves are typically 2 kg heavier than heifer calves. Similar trends have been documented in backcrosses (Roberson et al., 1986; Amen et al., 2007a; Dillon et al., 2015); however, potential reciprocal differences among F_2 generations are not yet known.

Bovine respiratory disease (BRD) is viewed as the greatest health threat to U.S. cattle feeding efficiency and profitability (Gifford et al., 2012). Reductions in ADG and hot carcass weight are common in steers with BRD (Schneider et al., 2009; Gifford et al., 2012). A disease component of BRD is bovine viral diarrhea (BVD), caused by the BVD virus (BVDV), which is prevalent in cattle populations worldwide (Peterhans et al., 2003), and results in economic losses for producers

(Ridpath et al., 2007). Cattle infected with BVDV have been shown to experience immunosuppression (Howard, 1990), including elements of the innate immune system (Peterhans et al., 2003). The BVD virus can replicate in monocytes and macrophages and suppresses the secretion of interleukin-1 (IL-1) (Jensen and Schultz, 1991).

It has also been speculated that relationships involving growth and health may be inversely related in livestock species. Dairy cattle that have been selected for high milk production have been found to have increased incidence of mastitis (Rauw et al., 1998), and layers selected for greater egg weights have been shown to have lower natural antibody titers (van der Klein et al., 2015). This type of antagonistic relationship has not been studied in beef cattle.

The overall objective of this thesis was to compare growth-related weight traits of birth weight, weaning weight, yearling weight and 15-mo weight in reciprocal cross F_2 steers and F_3 steers, and associated growth rates between these weights. Furthermore, these steers were evaluated in a health and feeding trial where they were challenged with bovine viral diarrhea virus (BVDV) type1b and evaluated for weight, ADG, rectal temperature and monocyte counts, and the relationships among these growth and health traits were determined.

LITERATURE REVIEW

The following review summarizes the literature regarding the relationships between livestock growth and health, the impacts of bovine viral diarrhea virus (BVDV) and bovine respiratory disease (BRD) on the U.S. beef feedlot industry, and genetic considerations of growth in beef cattle.

Relationships between Growth and Health

There is thought to be a tradeoff between disease resistance and production traits (Stear et al., 2001). Animals that have been selected for high production efficiency often have more immunological problems. Selection for high production efficiency may have resulted in correlated, undesirable responses in other traits. Dairy cattle selected for high milk production have increased incidence of mastitis, udder edema and foot rot compared to a randomly bred control line of dairy cattle (Rauw et al., 1998). In a line of purebred layers negative phenotypic correlations were found between natural antibody titers and body weight, egg weight and egg breaking strength (van der Klein et al., 2015). Brotherstone et al. (2007) found that in dairy cattle maximum growth rate was genetically correlated with health problems such as mastitis and lameness at first lactation.

Immune function is a life history trait that will trade off against other life history traits such as growth and reproduction (Colditz, 2008). Life history theory assumes that resources are limited and need to be distributed across maintenance, reproduction and growth, and once resources have been used for one of these purposes they are no longer available for use. Life history theory is often defined as a set of evolved physiological strategies and behaviors that influence fitness and the allocation of resources (Rauw, 2012). If resources are allocated towards an animal's immune function it reduces the resources available for other life history traits (Colditz, 2008). Similarly, animals selected for high production levels may allocate a greater amount of resources to production, leaving fewer resources for maintenance and immune function. This may explain why animals selected solely for high production have higher incidences of immunological problems (Rauw, 2012). When placed in an environment where resources are limited and not sufficient to sustain both high production levels and maintenance requirements, animals that have been selected for high production levels tend to allocate resources towards production and leave metabolic functions without sufficient resources (Knap, 2005).

The metabolic cost of an immune response to infection influences the availability of resources for other life history traits (Rauw, 2012). Mounting an immune response increases metabolism and activates immune cells and at the same time decreases nutrient availability due to anorexia and sickness behavior. Priorities for nutrient utilization are also shifted, making it difficult for nonimmune cells to utilize nutrients. Tissues can even be damaged by an excessive immune response (Colditz, 2008). In the case of mastitis, host immune reactions often damage the epithelial tissue of the mammary gland (Rauw, 2012).

Fever is an important part of the metabolic cost of an immune response. In mice, a rise of 1° C in body temperature can increase metabolic rate by 5% to 13% (Knap and Bishop, 2000). An immune response also triggers the release of hypothalamic and pituitary hormones and pro-inflammatory cytokines. These cytokines trigger anorexia and fever (Knap and Bishop, 2000). It has been estimated that 40% of the decrease in growth due to an immune response is due to anorexia (Colditz, 2001). Pro-inflammatory cytokines also up-regulate gluconeogenesis and down-regulate muscle accretion (Knap, 2000). Pro-inflammatory cytokines can also induce acute phase response, which alters the availability of nutrient in systemic circulation (Colditz, 2008). Nutrients are redirected away from meat, milk and wool accretion towards production of acute phase proteins in the liver (Colditz, 2001). In beef cattle, inflammation caused by bovine respiratory disease (BRD) decreases ADG and gain to feed ratio (G:F), resulting in major economic losses. Immune response to BRD shifts metabolism to promote the production of acute phase proteins, which may contribute to loss in performance (Gifford et al., 2012).

An animal's immune function is complex. A host's immune response to a pathogen can be broken down into two parts: resistance and tolerance. Resistance refers to an animal's ability to eliminate pathogens or prevent the invasion of pathogens, and tolerance refers to an animal's ability to limit the damage caused by the infection (Rauw, 2012). Although both types of response incur a metabolic cost, those costs are different. The metabolic costs involved in resistance include fever, anorexia and acute phase reaction. The metabolic costs of tolerance are more difficult to measure. Immune tolerance involves protein turnover and repair of tissues when damage cannot be prevented (Rauw, 2012).

Counterbalancing the metabolic cost of an immune response is the metabolic cost of disease. Low-grade infections can decrease growth hormone (GH) and insulin-like growth factor 1 (IGF-1) concentrations, both of which are necessary for protein accretion and muscle growth (Colditz, 2001). In dairy cattle, increasing incidence of health problems has caused a financial burden and decreased cow longevity (Rauw and Gomez-Raya, 2015).

Proper immune function is necessary for animals to be healthy and productive. Over-activation of the immune system diverts resources away from production and can adversely affect growth. Selection for both high productivity and disease resistance in breeding animals is necessary but difficult for several reasons. Selecting for resistance to a single disease may inadvertently confer susceptibility to another disease, and this approach is not likely to be economically efficient. Selection for resistance to multiple diseases may be possible by selecting for enhanced immune responsiveness (Stear et al., 2001). However, selecting solely for enhanced immune responsiveness will allocate resources away from production (Rauw, 2012). Immune responsiveness and high production levels must simultaneously be selected to create robust animals (Knap, 2005). However, selecting for both types of traits at the same time proves difficult, and it was envisioned that this is because they are inversely related (Colditz, 2008). Stear et al. (2001) proposed a selection index be used to enhance both immune response and production traits simultaneously in order to overcome the unfavorable association. Still, selecting for enhanced immune responsiveness may be difficult because traits associated with fitness, such as immune responsiveness, have low heritability (Bijma, 2009).

Bovine Viral Diarrhea Virus

Bovine viral diarrhea virus is prevalent in the beef cattle population worldwide (Peterhans et al., 2003) and causes economic losses for producers (Ridpath et al., 2007). Bovine viral diarrhea virus is classified in the *Pestivirus* genus and the *Flaviviridae* family (Bolin, 2002). First reported in 1946, BVDV is characterized by high fever, leukopenia (the reduction in circulating lymphocytes, monocytes and macrophages) and alimentary tract lesions (Ellis et al., 1998). Typical circulating monocyte counts in cattle are between 0 and 0.9 x 10^3/ µL (Aiello and Moses, 2015). There are two biotypes of BVDV, cytopathic and non-cytopathic (Howard, 1990). Cytopathic BVDV typically induces cell death whereas noncytopathic (ncp) BVDV often establishes itself within cells (Bolin, 2002). Cattle infected with ncp BVDV often experience immunosuppression (Howard, 1990). Part of this immunosuppression may be due to the ability of ncp BVDV to suppress elements of the innate immune system (Peterhans et al., 2003). Bovine viral diarrhea virus can replicate in monocytes and macrophages and suppresses the secretion of interleukin-1 (IL-1) (Jensen and Schultz, 1991). The release of pro-inflammatory cytokines such as IL-1 by monocytes and macrophages is essential for mediating an immune response. Cytokine release mediates pyrexia, anorexia, acute phase protein production by the liver and many other inflammatory responses necessary to remove pathogens (Day and Schultz, 2014). Bovine viral diarrhea virus and immunosuppression associated with the virus have long been thought to contribute to bovine respiratory disease (BRD) (Fulton et al., 2016). However, a recent viral metagenomics analysis on nasal secretions of dairy calves with BRD as well as controls did not detect BVDV or several other viruses traditionally associated with BRD, including PI3, BoCV and BRSV (Ng et al., 2015).

Bovine Respiratory Disease

In the U.S. beef industry, bovine respiratory disease (BRD) is viewed as the greatest health threat to cattle feeding efficiency and profitability (Gifford et al., 2012). The combination of treatment costs, death loss, and decreased gain to feed ratios (G:F) have been estimated to cost the beef industry $800 million to 900 million annually (Chirase and Greene, 2001). Steers with lung lesions due to BRD have returned a net $73.78 less than steers without lung lesions, and 21% was attributed to treatment costs and 79% was attributed to lighter hot carcass weight (HCW) and poorer quality grade (Gifford et al., 2012). Schneider et al. (2009) examined records from 5,976 animals in Midwestern feedlots. The authors found that overall incidence of BRD, when defined as cattle that had lung lesions, or were treated in the feedlot for BRD, or both, was 64.4%. They also found that BRD decreased ADG during the acclimation period by 0.37 kg and ADG across the entire feeding period by 0.07 kg. In a feedlot setting sick animals are identified and treated by pen riders. Visual detection of BRD is not always accurate. Pen riders must make judgment calls based on experience and outward signs of disease such as lethargy, nasal discharge or rough hair coat (Edwards, 2010).

Ng et al. (2015) evaluated dairy calves for a genome wide association study (GWAS) and found SNP effects explained 20% of the variation in BRD incidence; heritability for BRD susceptibility was estimated to be 13%. Heritability increases when the accuracy of the phenotype measured improves (Van Eenennaam et al., 2014). A better of understanding of the microorganisms that contribute to BRD would likely improve the understanding of genetic causes of susceptibility. Multiple viral and bacterial agents as well as management and environmental factors contribute to BRD, making diagnosis difficult.

Genetic Aspects of Growth

Breed and other genetic differences affect tissue growth, weight at the beginning of the fattening period and ratio of muscle to bone in beef cattle (Berg and Butterfield, 1968). Brown et al. (1972) found that Angus females reached their mature weight sooner than Hereford females and that Hereford females were on average 35 kg heavier at mature weight than Angus females. Earlier maturing breeds are expected to have lighter mature weights. Schenkel et al. (2004) evaluated Charolais, Limousin, Angus, Simmental, Hereford and Blonde d'Aquitaine bulls for the growth traits, ADG and weight over 140 days post weaning. These authors found significant breed differences for ADG and size with Charolais and Simmental having the heaviest metabolic weights (99.8 and 102.9 $kg^{0.75}$, respectively) and the highest ADG (1.87 and 1.82 kg/d respectively) and Hereford having the lightest metabolic weight (92.02 $kg^{0.75}$) and the lowest ADG (1.63 kg/d). Genetic differences for growth have also been found within a breed. Beltran et al. (1992) compared two lines of Angus cattle over many years. One line (Line A) was selected for heavy mature cow weight and the other was selected for rapid maturity (Line K). Cattle from Line A were heavier than those from Line K at birth, weaning, 18 months and maturity. However, cattle from Line K reached their mature weight at approximately 4.5 years of age, whereas cattle from Line A did not reach mature weight until approximately 5.5 years of age. Brahman influenced crossbred cows have been found to be even more delayed in reaching their mature weights. Cunningham (2013) found that Brahman crossbred cows were still increasing in weight at their fifth parity.

Heritability can be broadly defined as the fraction of the variance due to heredity rather than environment (Lush, 1940). The narrow sense heritability of a trait can be used as an indicator of the amount of progress expected to be made per generation by selection of parents (Lush, 1940; Lasley et al., 1961). The term "heritability" used in livestock breeding and genetic discussions refers to the narrow sense heritability. Heritability estimates for cattle weights and weight gain range from low to moderate (MacKinnon et al., 1991). Birth weight heritability estimates range from 0.16 to 0.61 (Quaas et al, 1985; MacKinnon et al., 1991; Meyer, 1992; Ahunu et al., 1997). Weaning weight heritability estimates range from 0.12 to 0.66 (Quaas et al., 1985; Brown et al., 1990; MacKinnon et al., 1991; Meyer, 1992). Yearling weight heritability estimates range from 0.25 to 0.31 (Mrode and Thompson, 1990; MacKinnon et al., 1991; Meyer, 1992. Post weaning ADG heritability estimates range from 0.28 to 0.35 (Arthur et al., 2001; Schenkel et al., 2004).

Many weight and growth traits are genetically correlated. Genetic correlations indicate whether or not a change in one trait is expected to result in the change of the other (Lasley et al., 1961). MacKinnon et al. (1991) estimated genetic correlations of birth weight with weaning weight and yearling weight to be 0.57 and 0.47, respectively, and the genetic correlation between weaning weight and yearling weight to be 0.84.

Other genetic effects also influence growth (Meyer, 1991). Maternal effects have a strong effect on the early growth of beef calves (Meyer et al., 1993). Meyer (1991) found that maternal effects contributed to 8.3 % of the total variation in birth weight in Angus and 10.1% in Hereford. Maternal effects were estimated to account for 29.1% of the total variation in weaning weight in Hereford cattle but only 12.5% in Angus. Maternal effects on growth and weight are usually associated with preweaning traits where milk production of the dam may be a limiting factor in growth of the calf (Meyer et al., 1993). However, maternal effects have been shown to carry over to some extent to post-weaning traits. Meyer (1991) found that maternal effects contributed to 5% of the total variance of final weight before slaughter.

Heterosis in both the calf and the dam can also affect weight and growth traits (Arthur et al., 1994). Heterosis is generally expected to be to proportional to the heterozygosity of an individual's gene pairs (Riley et al., 2005). According to the dominance model, loss of heterozygosity occurs between the F_1 and F_2 generations (Gregory et al., 1991). However, if inbreeding is avoided, further loss of heterozygosity is not expected to occur in later generations of random matings. In composite breeds the heterozygosity is expected to be proportional to (n-1)/n where n is the number of breeds that contribute equally (Gregory et al., 1993). However, SNP data do not support this dominance theory. Gill et al. (2009) found that only 0.8% of SNP were fixed for alternate alleles in Nellore and Angus. Arthur et al. (1994) found that direct heterosis resulted in increased weaning weight, yearling weight and both post- and pre-weaning ADG on high quality pasture. The F_1 Brahman-Herefords were 24.9 kg heavier at weaning than purebred Herefords and gained 79 g per day pre-weaning. The F_1 cattle were also 70.9 kg heavier at 26 months of age than the purebreds and gained 76 g per day post-weaning. Backcross calves were also found to have increased pre-weaning ADG of 31 g per day due to maternal heterosis.

Breed differences are important considerations for calf growth and size in crossbreeding systems (Sacco et al., 1990). Sanders et al. (2005) compared F_1 calves out of Hereford cows and Angus, Gray Brahman, Gir, Indu-Brazil, Nellore and

Red Brahman bulls for birth, growth, carcass and cow productivity traits and found that Red and Gray Brahman-sired calves were the heaviest at weaning, and Gir- and Angus-sired calves were the lightest. Paschal et al. (1995) evaluated calves out of the same matings for post-weaning growth and found that the *Bos indicus*-sired calves had higher post-weaning ADG than the Angus-sired calves. Among the *Bos indicus* influenced calves those sired by Red and Gray Brahmans had the highest post-weaning ADG and were the heaviest at a year of age. Herring et al. (1996) also compared different F_1 crosses. The study evaluated F_1 calves out of Angus and Hereford cows and Brahman, Boran and Tuli bulls for birth, growth, size, and carcass characteristics. Brahman-sired calves were found to have higher pre-weaning ADG than calves sired by Boran or Tuli bulls. Brahman-Angus F_1 bulls have also been found to be heavier than F_1 Senepol-Angus or Tuli-Angus bulls at a year of age (Chase et al., 2001).

In addition to breed, how the breed is incorporated through the type of mating may influence performance in crosses involving *Bos indicus* and *Bos taurus*. Xiang et al. (2003) found that parent-of-origin effects control myofiber development. Crossbred calves with a greater proportion of *Bos indicus* in the sire than in the dam have been shown to have heavier birth weights than the reciprocal cross. There has also been shown to be a greater difference in birth weight between males and females in calves that have a greater proportion of *Bos indicus* in the sire than the dam (Roberson et al., 1986; Amen et al., 2007a; Dillon et al., 2015). Crossbreds with a greater proportion of *Bos indicus* in the sire than the dam have also been shown to be heavier for weaning weight and feedyard entry weight than reciprocal crosses (Amen et al., 2007a,b). Preliminary results involving reciprocal F_2 Brahman-Hereford crosses suggest that calves out Hereford-Brahman sired F_2 cows were heavier at weaning than those out of Brahman-Hereford sired F_2 cows (Boenig, 2011). Rohrer et al. (1994) found no evidence that mitochondrial inheritance contributed to reciprocal differences at birth, weaning or yearling weights in Brangus calves.

Sex-specific genomic imprinting has been speculated to contribute to inheritance of reciprocal differences in *Bos indicus*-*Bos taurus* crosses (Dillon et al., 2015). Vrana (2007) crossed two species of mice within the genus *Peromyscus*. Female *P. maniculatus* crossed with male *P. polionotus* were found to produce neonates much smaller than either parental strain. Conversely, female *P. polionotus* crossed with male *P. maniculatus* were found to produce extremely large embryos much larger than either parent strain. The authors proposed that these differences were due to genomic imprinting. Zechner et al. (1997) also found that placental hyperplasia occurs in interspecific mouse crosses when the *Ihdp* (interspecific hybrid placental dysplasia) locus on the X chromosome of *M. macedonicus* interacts with autosomal loci of *M. musculus.*

Summary

Calves with a greater proportion of *Bos indicus* in the sire than the dam have been found to have heavier birth weights than the reciprocal cross. This is thought to potentially be a result of genomic imprinting and may involve the species source of X chromosome, as similar patterns have been observed as a result of matings of different species of *Peromyscus* mice. Preliminary results (Amen et al., 2007b; Boenig, 2011) show that these types of phenomena may affect later weights such as weaning weight in *Bos indicus x Bos taurus* crossbred calves as well.

Bovine viral diarrhea (BVD) is a component disease of bovine respiratory disease (BRD) complex and is characterized by pyrexia and leukopenia with immunosuppressive effects. The BVD virus has been found in monocytes of infected animals, potentially contributing to suppression of innate immune system function.

Growth and health have been speculated to be inversely related. Animals have a finite amount of nutritional resources to support cellular and metabolic functions, and once resources have been allocated towards one purpose they are no longer available to be used for another. Mounting an immune response can consume a large amount of resources. However, proper immune function is necessary for animals to be productive and healthy. Selecting animals solely on growth may result in animals that allocate resources toward growth at the expense of basic metabolic functions. Animals that have been selected heavily for growth have been shown to have increased instance of disease.

OBJECTIVES

Weights and health records among Nellore-Angus halfblood F_2 and F_3 steers were evaluated to compare: (1) weights and ADG from birth, at weaning, approximately a year of age, and during a 42-d health and feeding trial until 15 months of age, (2) monocyte counts after exposure to Bovine Viral Diarrhea Virus, and (3) relationships among monocyte counts and ADG. The different types of crosses that produced the steers were investigated for all traits to determine if there was an inverse relationship between growth and health aspects, and if the same relationship appeared to exist for the different crosses

MATERIALS AND METHODS

Nellore-Angus halfblood F_2 and F_3. steers (n = 372) were born between 2009 and 2012 as a component of the Texas A&M AgriLife Research McGregor Genomics Project. The F_2 steers were sired by F_1 Nellore-sired (NA) or Angus-sired (AN) bulls out of NA and AN F_1 dams, giving rise to 4 reciprocal calf types (ANAN, ANNA, NAAN, NANA, where the breed type of the bull is listed first). The F_3 steers resulted from F_2 NANA parents (bulls and dams). Weights were taken at birth, weaning (6 to 7 months age), approximately 365 d, and at multiple times throughout a health and feeding trial. Near 365 d of age steers were shipped from the Texas A&M AgriLife Research Center in McGregor, Texas to the TAMU Beef Cattle Systems Research facility in Burleson County, Texas where the health and feeding trial occurred.

Prior to the feeding trial all steers were tested to be free of Bovine Viral Diarrhea Virus (BVDV) persistent infection. Steers were stratified by sire and calf type across three bovine respiratory vaccine treatments and given a modified live vaccine, a killed vaccine, or no vaccine. At day 0 (28 to 35 d following vaccination, calves were vaccinated at a year of age so steers were 13 to 14 months at challenge) all steers were challenged intranasally with BVDV type 1b strain CA0401186a from the USDA-ARS National Animal Disease Center, Ames IA and were observed for many health and performance measures for 42 days. Steers were stratified by vaccine treatment across pen. Weights and hematology profiles were taken on d 0, 7, 14, 28 and 42. Runyan (2013) reported procedures in depth and summarized many of the performance measures from the health trial.

Weights and average daily gains (ADG) of animals at various periods from birth through the end of the 42-d health trial were analyzed using mixed model procedures. Weight at 15 months corresponded with the end of the 42 d health trial. Independent fixed effects to evaluate weights included calf type, age of dam, and the regression of age of the calf (or its Julian birthdate for birth weight). Sire and year were included as random effects. Vaccine type was also investigated as a fixed effect for weights taken during the feeding and health trial. Monocyte counts were available from d 0, 7, 14, 28 and 42 of the health and feeding trial and were evaluated through mixed models similar to the weight and ADG analyses. Weights, ADG and monocyte counts during the health trial were analyzed using repeated measures analysis. For fixed effects identified with $P \leq 0.10$ from F-tests, least squares means were separated by 2-tailed t-tests.

In addition to mixed model analyses, simple Pearson correlations among the weight, ADG and monocyte counts were determined. Correlations involving the change in monocyte count from d 0 (d 0 value – later d value) and the change in rectal temperature from d 0 (later d value – d 0 value) were also investigated as to their relationship with ADG during the 42-d health trial and during earlier life stages.

RESULTS AND DISCUSSION

The following results are provided in the order of calf weights, average daily gain (ADG) at various life stages, monocyte analyses, and finally correlations involving ADG with rectal temperature and monocyte counts, respectively.

Table 1 shows the summary statistics for the traits evaluated in this study. The number of animals in the health trial is lower than earlier traits because 15 steers were castrated later than planned and inadvertently vaccinated for BRD at weaning; their records were removed from the health trial.

Table 1. Summary statistics for weights, ADG and monocyte counts.

Trait	n	Simple mean	SD	CV	Min	Max
Birth weight, kg	378	35.7	6.5	18.1%	18.1	58.1
Weaning weight, kg	379	217.9	37.4	17.2%	107.0	302.0
Yearling weight, kg	378	273.8	47.0	17.2%	138.8	391.8
D 0[1] weight, kg	363	329.7	48.3	14.6%	191.4	458.1
D 3 weight, kg	361	328.7	48.4	14.7%	188.7	464.9
D 7 weight, kg	362	333.7	48.1	14.4%	195.0	471.7
D 10 weight, kg	361	334.7	47.6	14.2%	195.9	471.7
D 14 weight, kg	360	339.2	47.0	13.9%	200.5	476.2
D 28 weight, kg	363	361.4	48.0	13.3%	223.1	505.7
D 42 weight, kg	363	378.8	49.2	13.0%	237.6	526.1
ADG birth to weaning, kg/d	363	1.1	0.1	11.2%	0.6	1.6
ADG weaning to year, kg/d	363	0.3	0.2	67.9%	-0.5	0.8
ADG year to d 0, kg/d	363	1.1	0.4	39.3%	-0.3	3.6
ADG d 0 to d 14, kg/d	361	0.5	0.8	160.0%	-1.9	3.0
ADG d 14 to d 28, kg/d	360	1.6	0.6	38.3%	-1.6	3.2
ADG d 28 to d 42, kg/d	362	1.3	0.5	39.3%	-0.6	3.0
ADG d 0 to d 42, kg/d	363	1.3	0.4	27.9%	-0.5	2.1
Monocyte count d 0, 10^3	362	1.1	0.4	39.6%	0.4	3.4
Monocyte count d 7, 10^3	360	0.9	0.3	35.8%	0.3	2.3
Monocyte count d 14, 10^3	362	0.9	0.3	38.0%	0.3	2.4
Monocyte count d 28, 10^3	355	0.9	0.3	30.5%	0.3	1.9
Monocyte count d 42, 10^3	356	0.8	0.3	30.6%	0.4	2.2

[1] D 0, 7, 10, 14, 28, and 42 refers to timepoints during the 42-d health trial

Animal Weights

Significance levels of the effects in the weight models are reported in Table 2. Calf type was an important source of variation for weaning weight and yearling weight with a trend for 15-month weight (P = 0.075). Calf type was not a significant source of variation for birth weight. Previous studies of Roberson et al. (1986), Amen et al. (2007a) and Dillon et al. (2015) reported differences in calf type due to relative amounts of *Bos indicus* and *Bos taurus* in the sire vs. the dam; however, the amount of *Bos indicus* and *Bos taurus* was the same in the sires and dams in this study, only the maternal and paternal origins of breed influence differed. Year was a significant source of variation for all weights. Age of dam was an important source of variation for weaning weight, but not other weights. Steer age was an important source of variation for weaning, yearling and 15-month weights. For each day of age the steers were expected be approximately 0.60 to 0.85 kg heavier across these weights.

Table 2. Summary of significance levels and variance estimates from weight analyses from birth to start of health and feed trial.

	Birth weight, kg	Weaning weight, kg	Yearling weight, kg	15-mo weight, kg
Calf type	0.806	<0.001	0.028	0.075
Year	<0.001	<0.001	<0.001	<0.001
Age of dam	0.238	0.006	0.618	0.497
Day or age[1]	0.028	<0.001	<0.001	<0.001
Regression coefficient[1]	0.05 ± 0.022	0.81 ± 0.079	0.67 ± 0.112	0.63 ± 0.157

[1]Regression on Julian birth date for birth weight and age in d for other weights.

Least squares means for steer weights at different ages from birth to 15 months of age are reported in Table 3. The F_3 steers were significantly lighter (16 to 27.5 kg) than any of the F_2 calf types at weaning. At a year of age the NANA steers were not significantly heavier than the F_3 steers, but the F_3 steers were still the lightest of all the calf types. The NAAN steers were not significantly heavier than the other calf types, but they ranked the heaviest across all weights.

The F_3 steers may have ranked lighter than all the types of F_2 steers at weaning due to a loss in maternal heterosis as F_2 steers had F_1 dams while F_3 steers had F_2 dams. According to the dominance model, loss of heterozygosity occurs between the F_1 and F_2 generations (Gregory et al., 1991). Heterosis is generally expected to be to proportional to the heterozygosity of an individual's gene pairs (Riley et al., 2005).

Maternal effects have a strong influence on the early growth of beef calves (Meyer et al., 1993). Maternal effects on growth and weight are usually associated with preweaning traits where milk production of the dam may be a limiting factor in growth of the calf (Meyer et al., 1993). However, maternal effects have been shown to carry over to some extent to post weaning traits. Meyer (1991) found that maternal effects contributed to 5% of the total variance of final weight before slaughter. An additional consideration in this trial is that all the F_3 steers were sired by NANA F_2 bulls and out of NANA F_2 dams. The NANA steers ranked the lightest among the F_2 steers at all weights. The F_3 steers are most likely lighter at later weights do to their composition rather than carry over maternal effects. Least squares means are graphically provided in Figure 1 for steer weaning weights and Figure 2 for yearling weights to visually observe trends across calf type.

Table 3. Least squares means for steers weights from birth to 15 months of age.

Calf type[1]	N	Birth weight, kg	Weaning weight, kg	Yearling weight, kg	15-mo weight, kg
ANAN	23	34.6 ± 1.83	226.8 ± 6.14[a]	288.3 ± 9.37[a]	397.0 ± 12.91
ANNA	68	35.1 ± 1.29	229.8 ± 4.24[a]	286.9 ± 6.58[a]	392.3 ± 9.14
NAAN	31	36.6 ± 1.64	234.1 ± 5.47[a]	292.6 ± 8.36[a]	407.0 ± 11.62
NANA	62	36.4 ± 1.37	222.6 ± 4.50[a]	275.0 ± 6.98[b]	381.7 ± 9.70
F_3	188	35.2 ± 1.19	206.6 ± 3.91[b]	264.3 ± 6.05[b]	369.8 ± 8.40

[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents
[abc]Within a column, where superscripts are present means without a common superscript differ ($P < 0.05$).

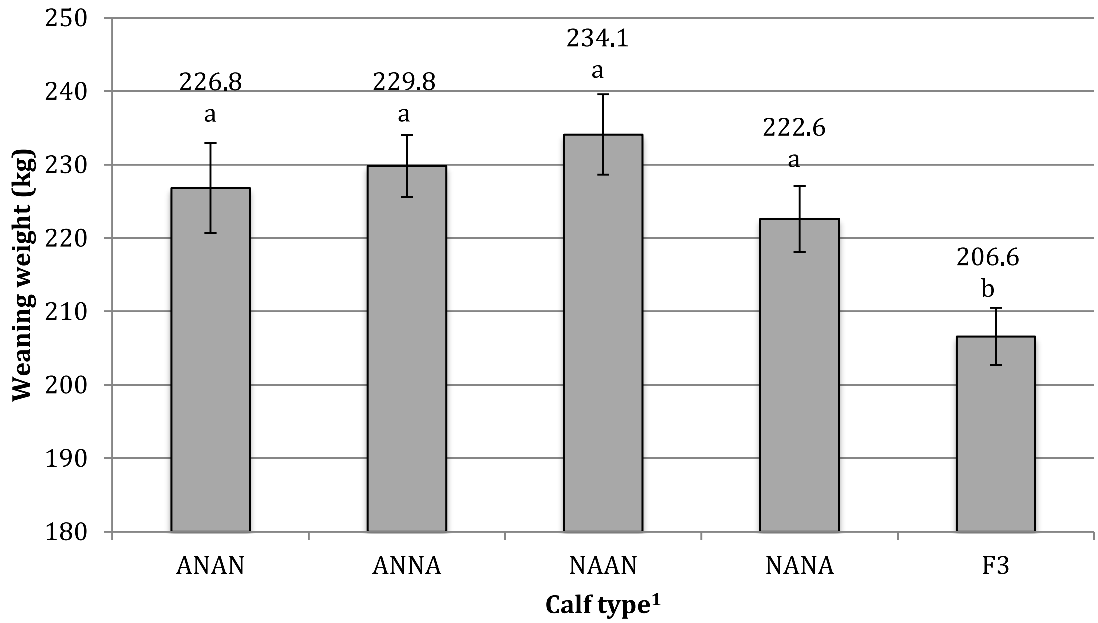

Figure 1. Least squares means for weaning weight across calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

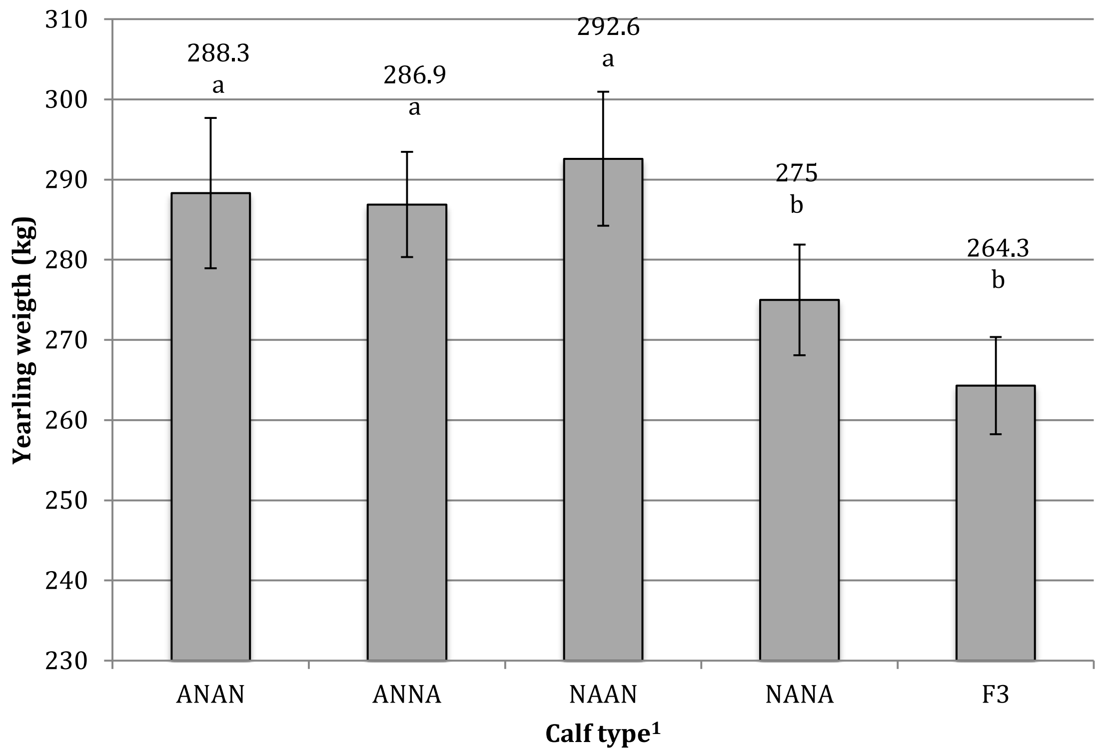

Figure 2. Least squares means for yearling weight across calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Summary of the weight least squares means across calf type for the health trial is provided in Table 4. The F_3 steers were the lightest ($P < 0.05$) calf type at all weights, and were approximately 15 to 20 kg lighter than the lowest ranking F_2 type (NANA) across these evaluation days. The F_2 steers out of AN dams typically ranked heavier than those out of NA dams throughout the trial, similar to the pattern seen in the pretrial weights. These results are somewhat similar to trends reported by Boenig (2011) where F_2 cows sired by F_1 Hereford-Brahman (HB) bulls on the HB cows weaned heavier calves than F_2 cows sired by F_1 Brahman-Hereford (BH) bulls on BH cows. This difference in weight ranking due to dam may be a result of sex specific genomic imprinting. Xiang et al. (2003) found that parent-of-origin effects control myofiber development in cattle. In mice, reciprocal differences for neonate weight among interspecific matings have been attributed to genomic imprinting. Vrana (2007) crossed two species of mice within the genus *Peromyscus*. Female *P. maniculatus* crossed with male *P. polionotus* were found to produce neonates much smaller than either parental strain. Conversely, female *P. polionotus* crossed with male *P. maniculatus* were found to produce extremely large embryos much larger than either parent strain. The authors proposed that these differences were due to genomic imprinting. There may also be an interaction with a locus on the X chromosome with a locus on an autosome. Zechner et al. (1997) reported that placental hyperplasia occurs in interspecific mouse crosses when the *Ihdp* (interspecific hybrid placental dysplasia) locus on the X chromosome of *M. macedonicus* interacts with autosomal loci of *M. musculus.* Genomic analysis was not conducted during this thesis but it may provide insight into the cause of the reciprocal differences.

Table 4. Least squares means for steer weights (kg) during the health trial.

Calf type[1]	n	Day 0	Day 3	Day 7	Day 10	Day 14	Day 28	Day 42
ANAN	23	345.9 ± 16.12	343.4 ± 16.12	347.5 ± 16.12	348.3 ± 16.12	352.6 ± 16.12	373.3 ± 16.12	389.4 ± 16.12
ANNA	68	341.0 ± 14.45	340.0 ± 14.45	342.9 ± 14.45	344.0 ± 14.45	349.6 ± 14.45	370.7 ± 14.45	389.5 ± 14.45
NAAN	31	345.8 ± 15.53	345.7 ± 15.53	353.7 ± 15.53	352.6 ± 15.53	357.9 ± 15.53	378.5 ± 15.53	398.8 ± 15.53
NANA	62	335.6 ± 14.61	332.8 ± 14.61	338.8 ± 14.61	340.6 ± 14.61	344.2 ± 14.61	366.1 ± 14.61	383.0 ± 14.61
F_3	188	319.3 ± 13.60	318.5 ± 13.60	323.6 ± 13.60	324.3 ± 13.60	329.2 ± 13.60	352.1 ± 13.60	368.7 ± 13.60

Significance levels and estimates for variance components regarding steer weights, ADG and monocyte counts during the 42-d health trial when analyzed as repeated measures are reported in Table 5. The weights were investigated individually by evaluation day to determine the sire variance at these specific time points for comparison to previous weights. Day or time period was an important source of variation in the model for weight, ADG and monocyte count ($P < 0.001$). Vaccine type was not a significant source of variation for any of these traits, but the interaction of time period and calf type was a significant source of variation for monocyte counts, and showed a trend for ADG. Calf type was a source of variation for monocyte counts ($P = 0.010$) and showed trends for weight ($P = 0.057$) and ADG ($P = 0.059$).

Table 5. Summary of significance levels and variance estimates for repeated measures analysis of steer weights and average daily gain analyses during health and feeding trial

Effect	Weight, kg	ADG, kg/d	Monocytes, 10^{3}/ µL
Day/ time period	< 0.001	< 0.001	< 0.001
Vaccine type	0.279	0.057	0.711
Calf type	0.057	0.059	0.010
Period × vaccine type	--	0.073	0.001
Period × calf type	--	0.103	--
Sire	191.69	0.003	0.011
Year	602.07	0.037	0.011
Calf ID	0.974	-0.199	0.410
Residual	1492.21	0.331	0.092

-- indicates that the effect was not investigated for that trait

Significance levels and estimates for variance components for steer weights from the 42-d health trial when evaluated by individual evaluation day are reported in Table 6. Calf type was a source of variation for weight on days 3, 7 and 10 (*P = 0*.037, *P* = 0.037, and *P* = 0.048, respectively) with a trend (*P* = 0.06) for days 0, 14, 28 and 42. Vaccine type and pen were not significant sources of variation for weights across these days.

Table 6. Summary of significance levels and variance estimates for steer weights across days of health and feeding trial

	Day 0	Day 3	Day 7	Day 10	Day 14	Day 28	Day 42
Calf type	0.062	0.037	0.037	0.048	0.055	0.057	0.054
Vaccine type	0.303	0.280	0.290	0.210	0.323	0.323	0.213
Pen	0.800	0.508	0.881	0.861	0.748	0.727	0.761
Sire	168.63	145.01	178.27	147.15	172.84	187.21	222.28
Year	805.47	740.98	721.34	651.12	560.27	431.38	424.83
Residual	1344.55	1402.72	1370.68	1414.36	1435.68	1578.0	1657.7

Steer weights from the repeated measures analysis are provided across health trial days in Figure 3. Weights on days 7 and 10 were the only weights not significantly different (*P* > 0.05). As the health and feeding trial progressed the weights of the steers increased 48.8 kg from d 0 to 42. However, weights increased more rapidly after d 14 than from d 0 to d 14, which corresponds to the expectation that steers should have cleared the virus around d 14. Laureyns et al. (2011)

reported on a group of 5 peripartum dairy cows diagnosed with BVDV type 1 that experienced sever leukopenia and diarrhea. Diarrhea subsided around d 11, and the total white blood cell count (WBC) recovered to a normal level by d 16. It is expected that weight and ADG would increase after d 14 because the steers would no longer be directing nutrients towards fighting the virus and could instead use those resources for growth.

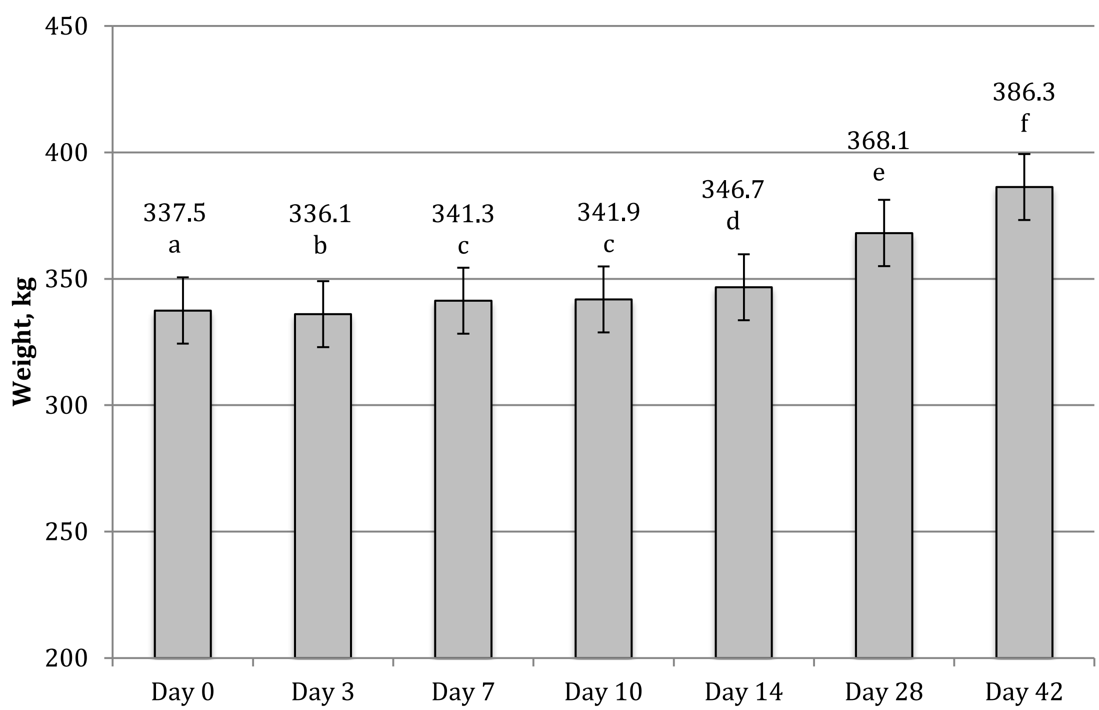

Figure 3. Steer weight across evaluation day evaluated as a repeated measure across 42-d health trial following BVDV challenge on d 0.

Figure 4 shows the least squares means of steer weights across the health trial due to calf type from the repeated measures analysis. Overall, the F_3 steers were significantly lighter (P < 0.05) than three of the four types of F_2 steers, but were not significantly different from NANA steers. The other types of F_2 steers were between 20.3 and 28.2 kg heavier than the F_3 steers. The F_2 steers out of AN dams were 3.5 to 13.1 kg heavier than F_2 steers out of NA dams across these 42 d.

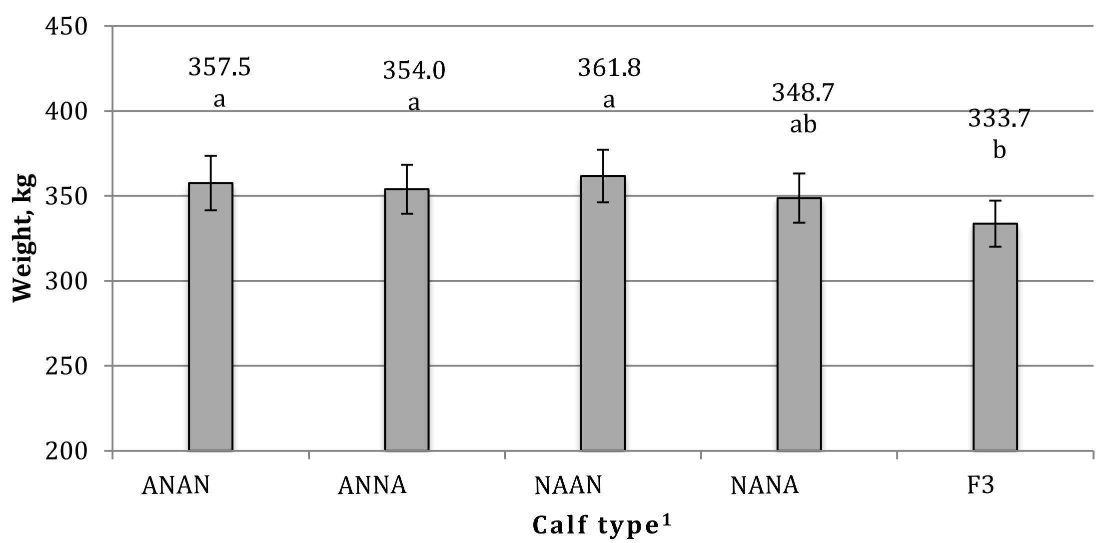

Figure 4. Least squares means of steer weight across calf type when evaluated as a repeated measure across the 42-d health trial.
[1]First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents

Average Daily Gain

Significance levels and estimates for variance components are reported in Table 7. Calf type was a significant source of variation for average daily gain from birth to weaning and average daily gain during the 42 day health and feeding trial, but did not have a significant effect on ADG from weaning to a year of age or from a year of age to the beginning of the health and feed trial. Dam age had a significant effect on the ADG of the calves from birth to weaning.

Table 7. Summary of significance levels and variance estimates from average daily gain analyses from birth through the health and feed trial.

	Birth to weaning, kg/d	Weaning to yearling age, kg/d	Yearling age to d 0 of health trial, kg/d	D 0 to d 42 of health trial, kg/d
Calf type	<.0001	0.597	0.927	0.051
Dam age	0.023	0.521	0.135	--
Sire variance	0.0008	0.0008	0.0221	0.004
Year variance	0.0008	0.0425	0.0453	0.042
Residual variance	0.0117	0.0148	0.1465	0.093

-- indicates that the effect was not investigated for that trait

Least squares means separated by age of dam for calf ADG from birth to weaning and weaning to a year of age are given in Table 8. Calves with dams between 5 and 9 years of age typically had the highest pre-weaning average daily gain and means across dam ages 11 to 15 were very similar.

Table 8. Effect of dam age on calf's average daily gain from birth to weaning and from weaning to a year of age.

Dam age, yr	n	Birth to weaning, kg/d	Weaning to year of age, kg/d
3	46	1.08 ± 0.024	0.32 ± 0.105
4	65	1.14 ± 0.022	0.31 ± 0.105
5	61	1.17 ± 0.024	0.28 ± 0.105
6	34	1.17 ± 0.028	0.26 ± 0.107
7	42	1.19 ± 0.030	0.25 ± 0.107
8	16	1.20 ± 0.037	0.28 ± 0.110
9	6	1.29 ± 0.053	0.26 ± 0.118
10	11	1.06 ± 0.042	0.38 ± 0.112
11	21	1.12 ± 0.033	0.28 ± 0.108
12	25	1.11 ± 0.030	0.31 ± 0.107
13	21	1.12 ± 0.032	0.33 ± 0.108
14	21	1.11 ± 0.037	0.32 ± 0.110
15	4	1.11 ± 0.060	0.35 ± 0.122
16	1	0.99 ± 0.114	0.34 ± 0.163
17	2	1.16 ± 0.080	0.36 ± 0.136

Figure 5 shows the least squares means for steer pre-weaning ADG. The general trend for ADG was similar to that of weaning weight. The F_3 steers had significantly lower average daily gain from birth to weaning than all four types of F_2 steers and gained between 0.10 and 0.13 kg/d less than F_2 steers.

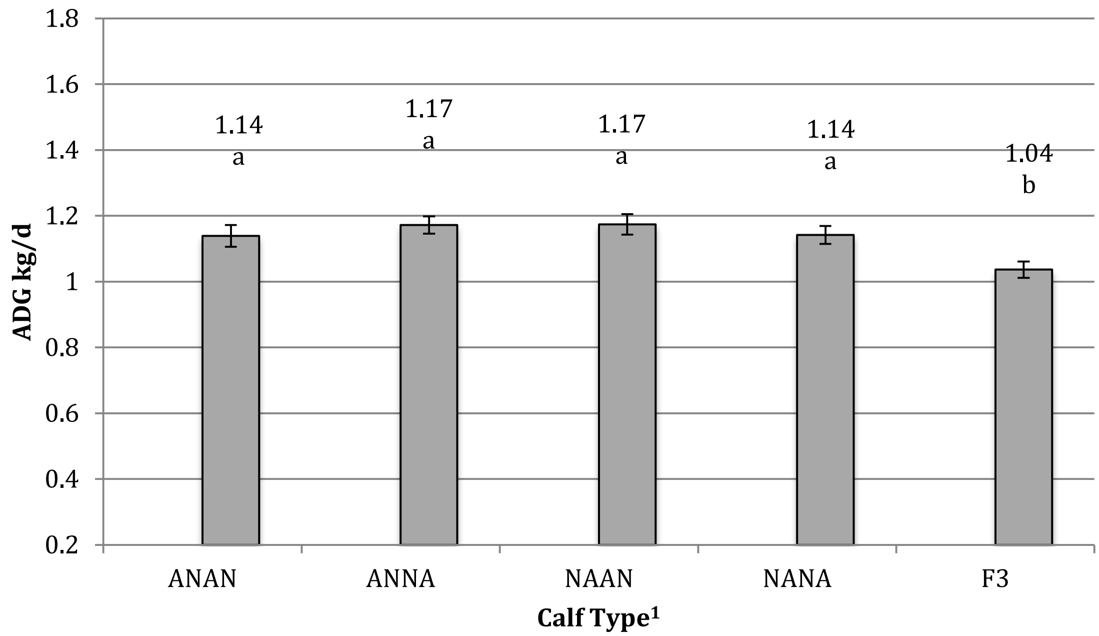

Figure 5. Least squares means of average daily gain (kg/day) from birth to weaning by calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents

Figure 6 shows least squares means for average daily gain from weaning to a year of age due to calf type. There was no significant difference between calf types for average daily gain from weaning to a year of age. The steers gained very little during this time period and the lack of significant difference may be a result of the overall means being low.

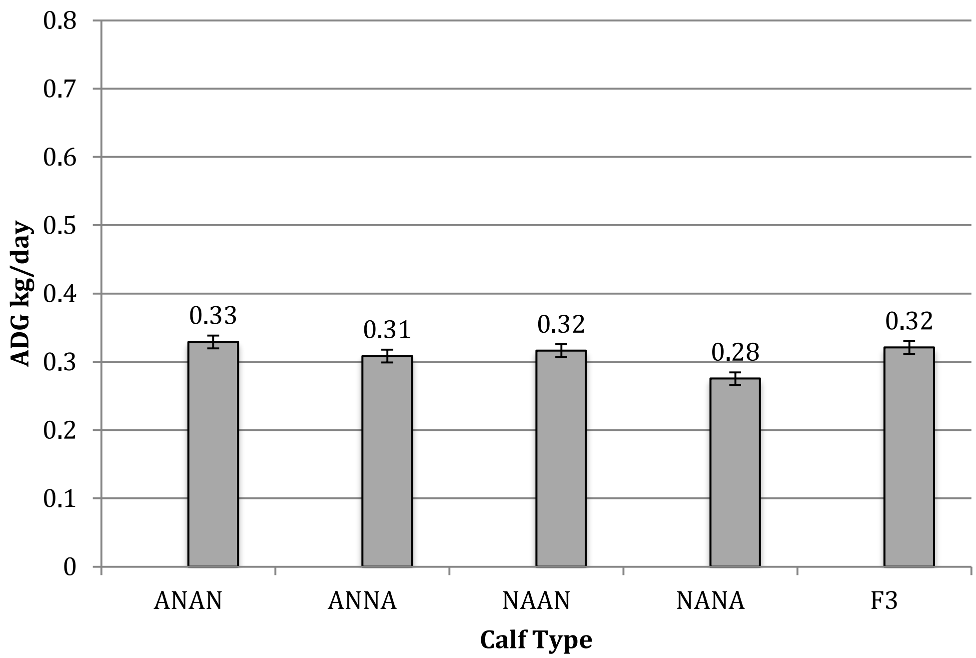

Figure 6. Least squares means of average daily gain (kg/d) from weaning to a year of age by calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Significance levels for fixed effects and estimates for variance components are located in Table 9. Calf type was not a significant source of variation for average daily gain during any of the three periods of the feed trial. Vaccine type had an effect (P = 0.017) on average daily gain during the first period of the feed and health trial. Steers that received a modified live vaccine gained 0.2 kg/d more than steers that received either a killed vaccine or no vaccine during the first period of the feed trial.

Table 9. Summary of significance levels and variance estimates for average daily gain during each of three periods of the 42-d health and feed trial.

	D 0 to 14, kg/d	D 14 to 28, kg/d	D 28 to 42, kg/d
Calf type	0.147	0.903	0.067
Vaccine type	0.017	0.772	0.085
Pen	0.709	0.001	0.430
Year variance	0.113	0.063	0
Sire variance	0.004	0.020	0.004
Residual variance	0.3850	0.304	0.232

Average daily gains for the steers from the repeated measures analysis are provided across time period in Figure 7. Average daily gain was significantly different among all three periods of the feed trial. Average daily gain was the highest during the second period of the feed and health trial and lowest during the first period of the feed and health trial. These results seem to correspond to those of Schneider et al. (2009) where steers that had BRD lung lesions at slaughter had ADG during the feedlot acclimation period decreased by 0.37 kg and ADG across the entire feeding period decreased by 0.07 kg.. Roeber et al. (2001) evaluated calves in the feedlot and found that calves treated for illness had 12% lower ADG for the first 67 d in the feedyard than calves that did not require treatment. However, ADG for treated and untreated calves was not different across all 185 d in the feedyard. Gardner et al. (1999) also reported that steers treated for BRD in the feedlot had 0.06 kg/d less ADG than untreated steers across the entire finishing phase.

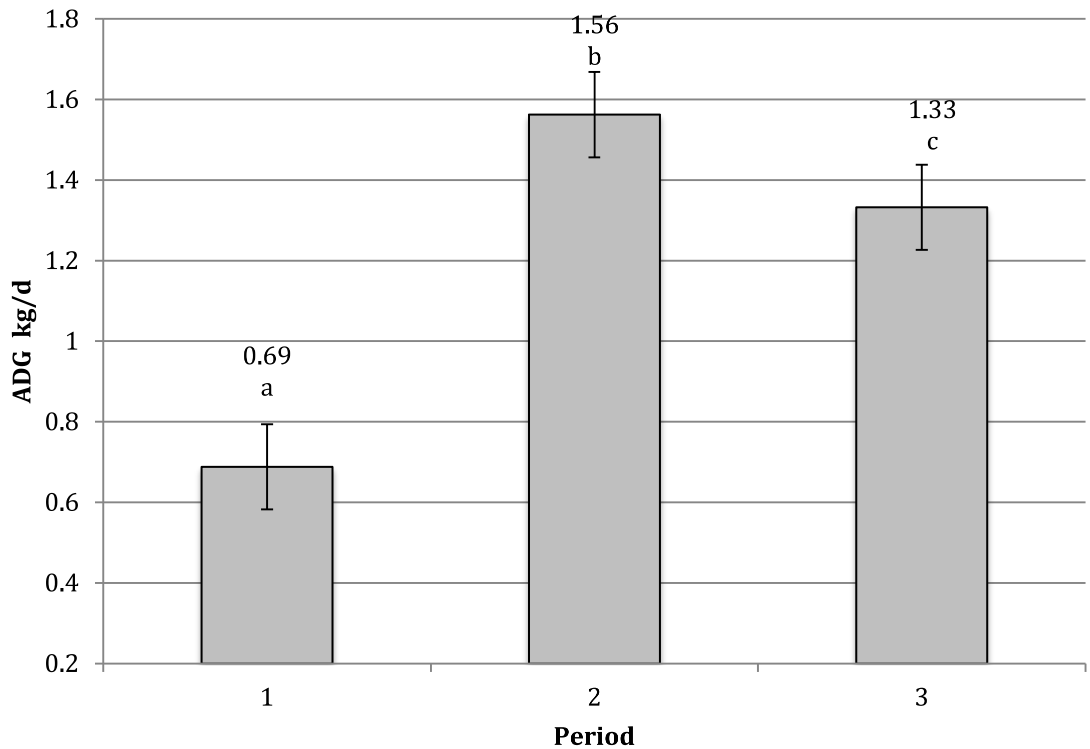

Figure 7. Least squares means of average daily gain (kg/d) analysis by repeated measures for the three two-week periods of the 42 day feed and health trial.

Average daily gains for the steers from the repeated measures analysis are provided across vaccine type in Figure 8. Average daily gain was significantly different between steers treated with the killed vaccine and steers treated with the modified live vaccine, but the average daily gain of the steers treated with either vaccine type was not significantly different from the average daily gain of the steers that did not receive a vaccine.

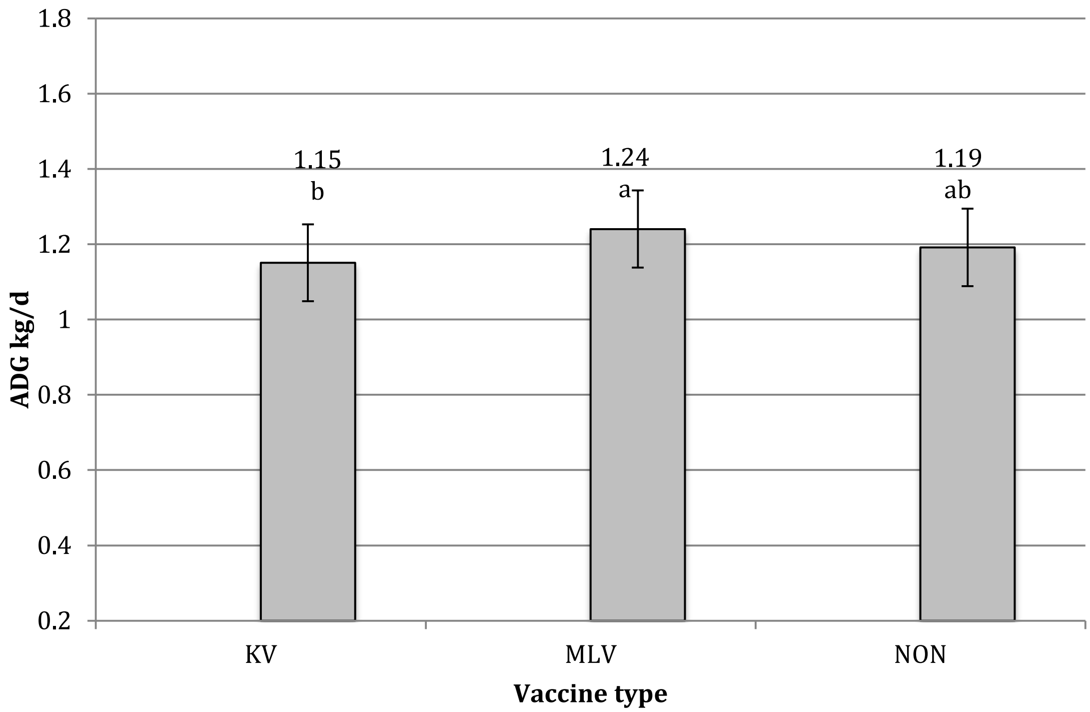

Figure 8. Least squares mean of average daily gain (kg/d) analysis by repeated measures during the health and feed trial by vaccine type.

Steer ADG from the repeated measures analysis are provided across calf type in Figure 9. The F_2 steers out of AN dams gained approximately 0.1 kg more per day than those out of NA dams.

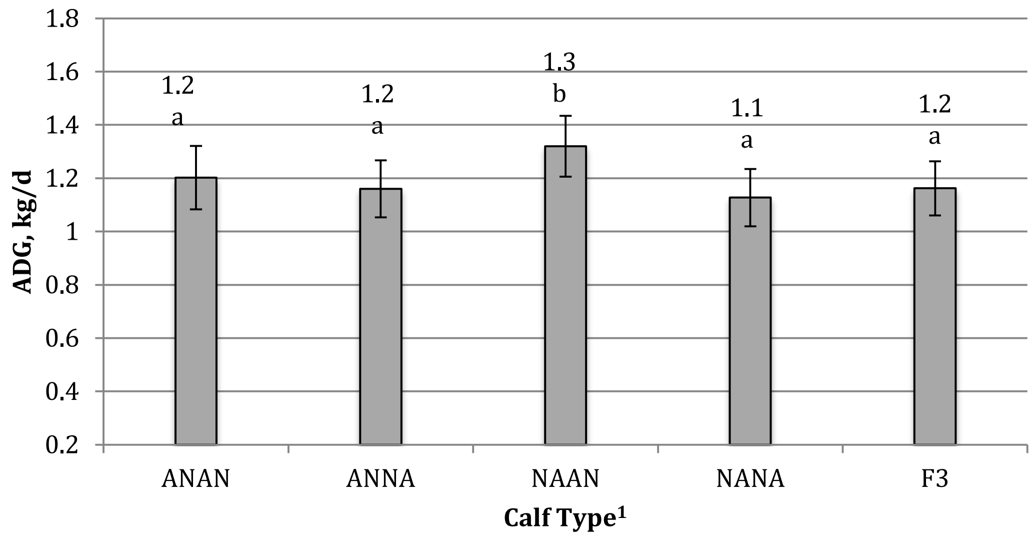

Figure 9. Least squares means of average daily gain (kg/d) analysis by repeated measures during the health and feed trial by calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Steer ADG from the repeated measures analysis are provided for the interaction between time period and vaccine type in Table 10. Time period had a significant effect on average daily gain across all three vaccine treatments. Average daily gain was highest during the second period and lowest during the first. During the first time period steers that received a modified live vaccine had significantly higher average daily gain than steers that received a killed vaccine or no vaccine. There were no differences in gain among the vaccine treatments during the later periods.

Table 10. Least squares means of average daily gain (kg/d) analysis by repeated measures during the feed and health trial by 2 week period and vaccine type.

Period	Killed	MLV	Non-vaccinated
1	0.62 ± 0.114^{ax}	0.82 ± 0.114^{ay}	0.62 ± 0.115^{ax}
2	1.58 ± 0.114^{b}	1.53 ± 0.114^{b}	1.57 ± 0.115^{b}
3	1.25 ± 0.114^{c}	1.37 ± 0.114^{b}	1.38 ± 0.115^{c}

^{abc}Within a column, means without a common superscript differ ($P < 0.05$).
^{xy} Within a row, means without a common superscript differ ($P < 0.05$).

Steer ADG from the repeated measures analysis for the interaction between time period and calf type in Table 11. All calf types had significantly lower average daily gain during period one than period two. Calf type NAAN had significantly higher average daily gain during the first period of the health trial than the other calf types. There was no difference among the calf types for average daily gain during the second period. During the third period F_2 steers out of AN dams gained between 0.13 and 0.21 more kg/d than F_2 steers out of NA dams

Table 11. Least squares means of average daily gain (kg/d) analysis by repeated measures during the feed and health trial by 2 week period and calf type.

Calf type	Period 1	Period 2	Period 3
ANAN	0.59 ± 0.160^{az}	1.59 ± 0.160^{b}	1.43 ± 0.160^{byz}
ANNA	0.61 ± 0.125^{az}	1.53 ± 0.125^{b}	1.34 ± 0.125^{byz}
NAAN	0.93 ± 0.14^{ay}	1.53 ± 0.145^{b}	1.51 ± 0.145^{bz}
NANA	0.62 ± 0.126^{az}	1.56 ± 0.126^{b}	1.20 ± 0.126^{cy}
F_3	0.69 ± 0.108^{az}	1.61 ± 0.108^{b}	1.18 ± 0.108^{cy}

[1]First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

^{abc}Within a row, where superscripts are present means without a common superscript differ ($P < 0.05$).

^{yz}Within a column, where superscripts are present means without a common superscript differ ($P < 0.05$).

Monocytes

Steer monocyte counts from the repeated measures analysis are provided across day in Figure 10. Monocyte counts at d 0 and 7 were significantly higher than at the later days of the trial. This decrease from d 0 to d 7 is similar to the findings of Ellis et al. (1998) where monocytes counts dropped at day 7 or 8 of infection. In the Holstein bull calves evaluated by Ellis et al. (1998) monocyte cell counts decreased approximately 25% at d 7 or 8 compared to pre-inoculation values, whereas there was approximately 10% reduction at d 7 and 18% reduction at d 14 among the halfblood steers in this trial.

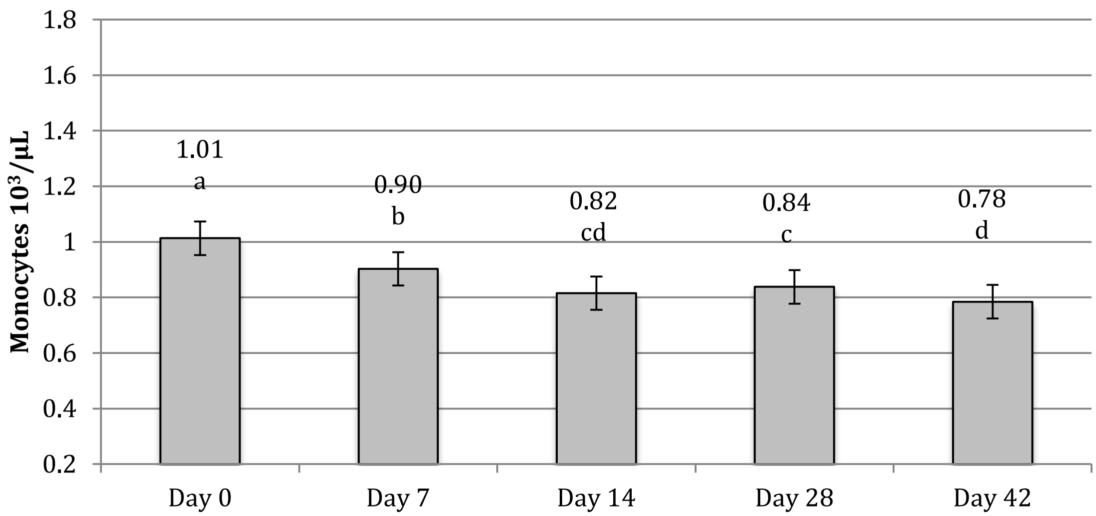

Figure 10. Least squares means of monocyte counts (x 10^3/µL) analysis by repeated measures during the health and feed trial by day

Steers monocyte count least squares means from the repeated measure analysis for day by vaccine type interaction are provided in Table 12. Across all three vaccine treatments monocyte counts were highest at d 0 and decreased as the trial progressed. At d 7 the steers that did not receive a vaccine had significantly lower monocyte counts than the steers that received either the modified live or killed vaccine.

Table 12. Least squares means of monocyte counts (x $10^3/\mu L$) analysis by repeated measures during the health and feed trial by vaccine type and day.

Vaccine type	D 0	D 7	D 14	D 28	D 42
KV[1]	1.05 ± 0.065^{x}	0.93 ± 0.065^{by}	0.83 ± 0.065^{z}	0.83 ± 0.065^{z}	0.78 ± 0.065^{z}
MLV	0.99 ± 0.065^{x}	0.97 ± 0.065^{bx}	0.80 ± 0.065^{y}	0.83 ± 0.065^{y}	0.80 ± 0.065^{y}
NON	1.00 ± 0.066^{x}	0.81 ± 0.066^{ayz}	0.83 ± 0.066^{yz}	0.85 ± 0.066^{y}	0.78 ± 0.066^{z}

[ab]Within a column, where superscripts are present means without a common superscript differ ($P < 0.05$).

[xyz]Within a row, where superscripts are present, means without a common superscript differ ($P < 0.05$).

[1]KV indicates a killed vaccine was administered; MLV indicates a modified live vaccine was administered; NON indicates no vaccine was administered

Steer monocyte count least squares means from the repeated measures analysis are provided across calf type in Figure 11. The F_2 steers out of AN dams had 0.02 to 0.15 x $10^3/\mu L$ higher monocyte counts than the F_2 steers out of NA dams. It is of interest that the F_2 steers out of AN dams ranked the heaviest for weights and also ranked the highest for monocyte counts. Whether or not these traits may be influenced by parent of origin effect, such as of control myofiber development reported by Xiang et al. (2003), remains uncertain.

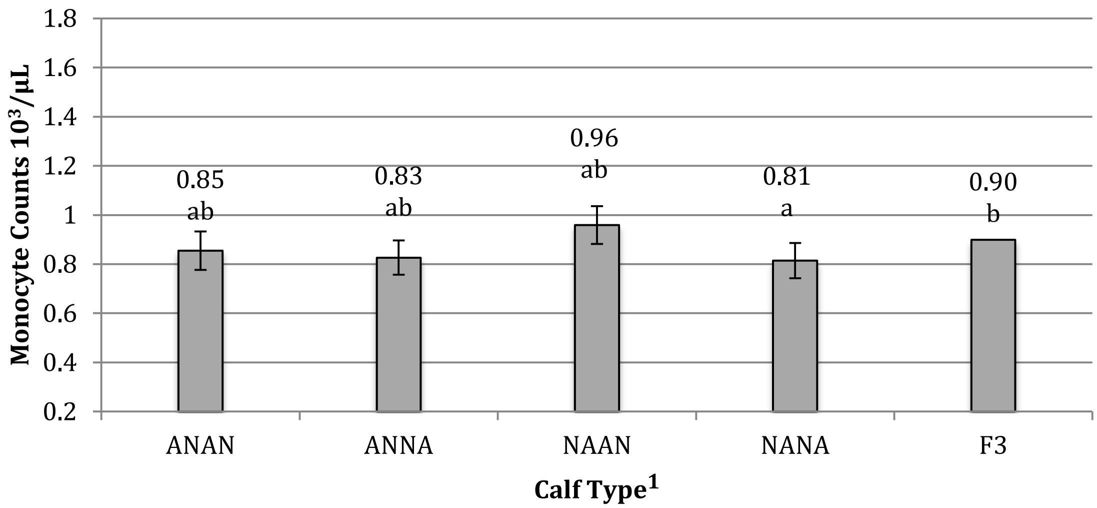

Figure 11. Least squares means of monocyte counts (x 10^3/µL) analysis by repeated measures during the health and feed trial by calf type.
[1]First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Correlation coefficients and significance levels for ADG prior to the health trial are provided in Table 13. Average daily gain from birth to weaning is significantly positively correlated with ADG from weaning to a year of age and average daily gain from a year of age to d 0 of the health trial. Average daily gain from weaning to a year of age is significantly negatively correlated with average daily gain from a year of age to d 0 of the health trial.

Table 13. Correlation coefficients and significance levels for ADG (kg/d) at different stages of steers' lives.

	ADG weaning to yearling	ADG yearling to d 0	ADG d 0 to d 14	ADG d 14 d 28	ADG d 28 to d 42	ADG d 0 to d 42
ADG birth to weaning	0.21 <0.001	0.17 0.002	-0.12 0.025	-0.05 0.33	0.03 0.605	-0.10 0.057
ADG weaning to yearling		-0.36 <0.001	-0.28 <0.001	-0.29 <0.001	0.02 0.705	-0.37 <0.001
ADG yearling to d 0			0.07 0.193	0.123 0.021	0.086 0.102	0.16 0.002
ADG d 0 to d 14				-0.00 0.955	0.03 0.540	0.72 <0.001
ADG d 14 to d 28					-0.24 <0.001	0.49 <0.001
ADG d 28 to d 42						0.37 <0.001

Correlation coefficients vary in direction and magnitude for different life stages of these steers. There may be different relationships between ADG at different time periods. Average daily gain from birth to weaning and weaning to yearling age are moderately positively correlated. These traits are most likely genetically correlated. Genetic correlations of birth weight with weaning weight and yearling weight have been estimated to be 0.57 and 0.47, respectively, and the genetic correlation between weaning weight and yearling weight to be 0.84. Average daily gain during the health trial have a different relationship than early traits. Average daily gain from d 0 to d 14 is not significantly correlated to ADG during the later two periods of the health trial. Calves are expected to be actively fighting the virus during the first 14 d post-challenge. Pyrexia and leukopenia associated with BVDV have been typically observed to resolve after d 14 (Ellis et al., 1998). Average daily gain may be lower during this time because resources are being redirected away from growth towards mounting an immune response. After the calves have cleared the virus they may enter a period of compensatory gain.

These relationships between ADG at different stages may also be a result of nonlinear growth curves of these animals. Correlation coefficients measure linear relationships between two time points and a linear relationship may not be the best representation of the actual growth of these animals. Least squares means of the steers' weights from weaning to the end of the health trial are provided graphically in Figure 12. The lines in this figure represent the steers' growth over time, which does not appear to be linear across long periods of time. There also appears to be some differences between the calf types, similar to the findings of Beltran et al. (1992), which found differences in growth curves for two different lines of Angus cattle. The two lines of Angus cattle had similar shapes to their growth curves but the line selected for heavier mature weight were shifted higher on the y axis.

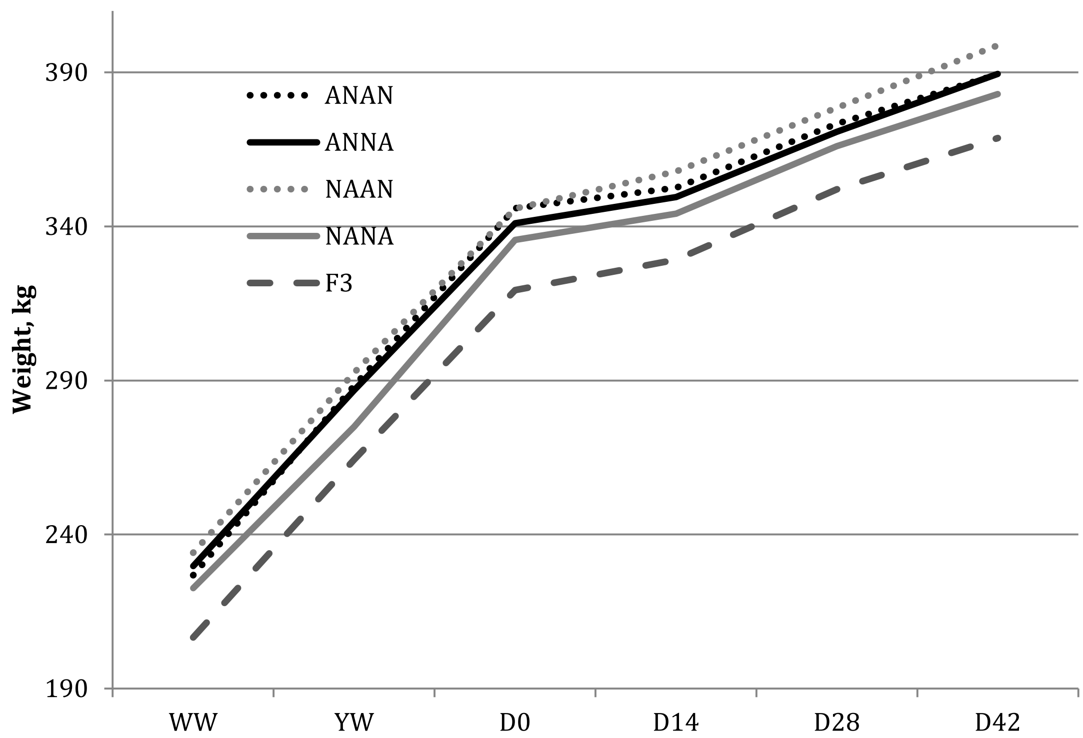

Figure 12. Least squares means of calf weights from weaning to d 42 of the health trial by calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Correlation coefficients and significance levels for monocyte counts (10^3) during the health trial are provided in Table 14. Monocyte counts for all days were significantly positively correlated with correlation coefficients between 0.41 and 0.57. Monocyte counts at all days had the strongest correlation d 28.

Table 14. Correlation coefficients and significance levels for monocyte counts (10^3/ µL) during the health trial.

	D 7	D 14	D 28	D 42
D 0	0.43 <0.001	0.44 <0.001	0.50 <0.001	0.41 <0.001
D 7		0.43 <0.001	0.51 <0.001	0.43 <0.001
D 14			0.57 <0.001	0.41 <0.001
D 28				0.53 <0.001

Based on previous speculation that growth and health may have antagonistic relationships, correlations of monocyte counts with ADG (pre-health trial and during BVDV challenge) were evaluated. Correlation coefficients and significance levels for average daily gains pre-health trial and monocyte counts during the health trial and provided in Table 15. Preweaning ADG was not related to monocyte count at any time following BVDV challenge. Average daily gain from weaning to a year of age was marginally, positively correlated with monocyte counts at d 0, 7 and 14 with a trend for d 28 (P = 0.09). There was a trend for ADG between yearling weight and d 0 of the health trial to have a small, negative correlation with monocyte count on d 0 (P = 0.09) and d 7 (P = 0.07). There were no significant correlations between monocyte counts and ADG during any of the three 14-d periods of the health and feed trial.

Table 15. Correlation coefficients and significance levels for average daily gain (kg/d) before the health trial and monocyte counts (10^3/ µL) during the health trial.

	Monocyte count				
Correlation	d 0	d 7	d 14	d 28	d 42
ADG birth to weaning	0.02 0.640	0.04 0.490	0.08 0.144	0.04 0.461	0.03 0.551
ADG weaning to yearling weight	0.18 0.001	0.14 0.008	0.13 0.010	0.09 0.091	0.04 0.487
ADG yearling weight to d 0	-0.09 0.092	-.10 0.069	-0.03 0.498	-0.04 0.425	-0.06 0.247

Summary statistics for change in rectal temperature during the health trial are provided by calf type in Table 16. Change in rectal temperature was calculated as the later d temperature minus the calf's temperature at d 0. A positive value indicates an animal had a higher temperature at the later d than it had on d 0. CV is large as a result of the simple means being small and the standard deviations being large.

Table 16. Summary statistics for change in rectal temperature during the health trial.

Day	n	Simple mean	SD	CV	Min	Max
			ANAN[1]			
D 3	22	0.16	0.55	344%	-1.00	1.72
D 7	22	0.18	0.72	400%	-1.11	1.67
D 10	22	-0.11	0.40	364%	-0.83	0.50
D 14	22	-0.10	0.47	470%	-0.72	0.83
D 28	22	0.06	0.55	917%	-1.06	1
D 42	22	0.08	0.51	638%	-0.83	1.06
			ANNA			
D 3	62	0.02	0.59	2950%	-1.39	1.61
D 7	62	0.07	0.61	871%	-1.22	1.78
D 10	62	-0.25	0.54	216%	-1.22	1.28
D 14	61	-0.14	0.53	379%	-1.28	1.39
D 28	61	-0.07	0.54	771%	-1.28	1.39
D 42	61	-0.06	0.62	1033%	-1.89	1.39
			NAAN			
D 3	31	0.14	0.58	414%	-0.89	1.33
D 7	31	0.03	0.60	2000%	-1.06	1.44
D 10	31	-0.27	0.61	226%	-1.67	0.89
D 14	31	-0.09	0.52	578%	-1.33	1.22
D 28	31	-0.02	0.54	2700%	-1.33	0.83
D 42	31	-0.01	0.73	7300%	-1.56	1.17
			NANA			
D 3	57	-0.07	0.60	857%	-1.61	1.22
D 7	57	-0.06	0.66	1100%	-1.56	1.94
D 10	57	-0.27	0.54	200%	-1.67	1.06
D 14	57	-0.26	0.64	246%	-2.06	0.89
D 28	57	-0.21	0.62	295%	-2.28	1.11
D 42	57	-0.17	0.64	376%	-2.28	0.94
			F_3			
D 3	186	0.11	0.66	600%	-1.39	2.00
D 7	186	-0.01	0.66	6600%	-1.61	2.17
D 10	185	-0.22	0.55	2750%	-1.94	1.56
D 14	186	-0.13	0.63	485%	-1.78	1.94
D 28	185	0.04	0.67	1675%	-1.89	2.67
D 42	185	0.05	0.67	1340%	-1.67	1.94

[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

Steers with a rectal temperature over 40° C are typically treated for BRD in commercial feed yards (Edwards, 2010). During the health trial any steers found to have a rectal temperature greater than 40° C were treated with an antibiotic (Runyan, 2013). The number of steers that had a rectal temperature greater than 40° C during the first 14 days is provided by calf type in Table 17.

Table 17. Frequency table of steers that had rectal temperature of 40°C between d 0 and d 14 of the health trial.

Calf Type	n total	n with rectal temp over 40°C on d 0	Percentage of calf type with rectal temp over 40°C on d 0	n with rectal temp over 40°C between d 1 and d 14	Percentage of calf type with rectal temp over 40°C between d 1 and d 14
ANAN	22	5	22.7%	13	59.1%
ANNA	62	19	30.6%	35	56.5%
NAAN	31	12	38.7%	20	64.5%
NANA	57	23	40.4%	31	54.4%
F_3	186	73	39.2%	113	60.8%

As rectal temperature is commonly used to aid in diagnosis of BRD, correlations involving change in rectal temperature from d 0 (when BVDV challenge was administered) to later d 7 and ADG were evaluated. After challenge with BVDV, calves have been observed to have the highest rectal temperature around 7 d after challenge. Ridpath et al. (2007) reported temperature peaked twice, at d 3 and between d 6 and 8 with this same BVDV strain in Holstein calves. Ellis et al. (1998) also observed that calves developed fever at d 3 and developed unremitting fever (40.5 to 41.6 °C) between d 6 and 8.

Correlation coefficients ($P < 0.05$) between the change in rectal temperature from d 0 to d 7and ADG for the different calf types are provided in Figure 13. As calf type was a significant source of variation for ADG at different life stages, the correlations between ADG and rectal temperature change after BVDV challenge per calf type were of interest.

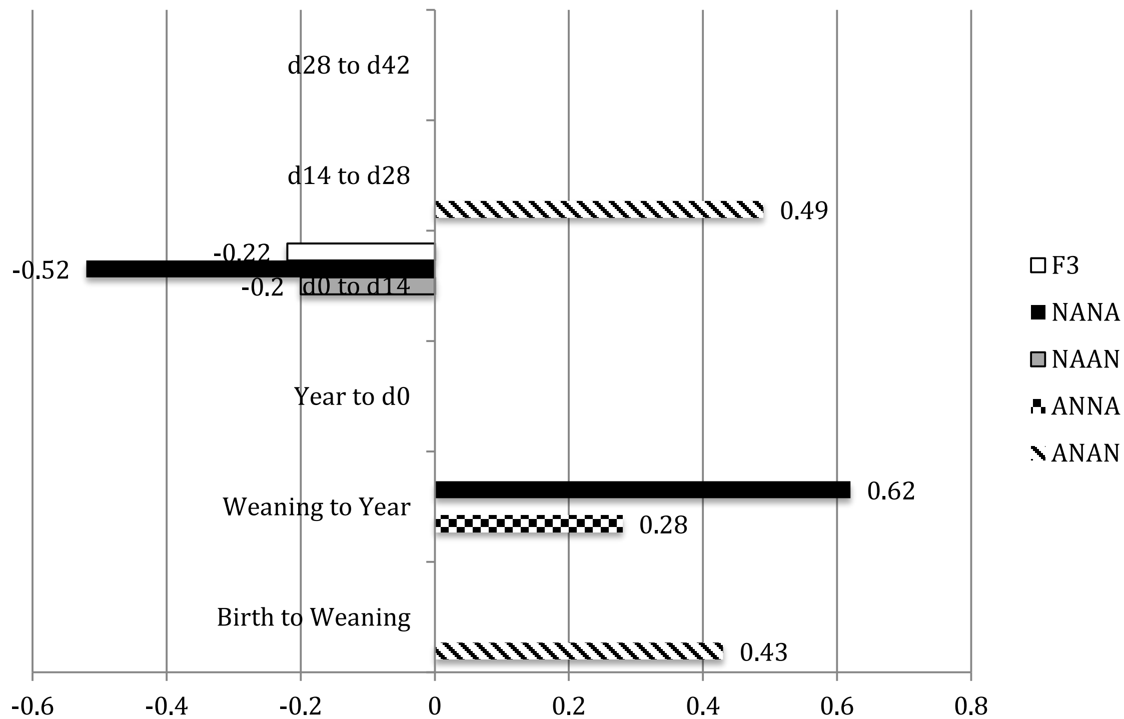

Figure 13. Correlation coefficients (P < 0.05) between rectal temperature change between d0 and d7 (d7-d0) and ADG at different life stages by calf type.
[1] First 2 letters describe F_1 sire type as Angus-sired (AN) or Nellore-sired (NA) and second 2 letters describe F_1 dam type (AN or NA); F_3 were produced from NANA F_2 parents.

It appears that some different patterns of relationship may exist between rectal temperature change and ADG among the different calf types. Among the ANAN steers rectal temperature change at d 7 was positively correlated with ADG from birth to weaning and ADG from d 24 to d 28 of the health trial. Average daily gain from weaning to a year of age was positively correlated with rectal temperature change among the ANNA and NANA steers. Average daily gain from d 0 to d 14 of the health trial was negatively correlated with rectal temperature change for NAAN and NANA steers. In Ridpath et al. (2007) temperature peaked twice, at d 3 and between d 6 and 8. Ellis et al. (1998) also observed that calves developed fever at d 3 and developed unremitting fever (40.5-41.6 °C) between d 6 and 8. The negative correlation may be a result of an increase in rectal temperature between d 0 and d 7 and a loss in ADG. Fever is part of an animal's immune response to a pathogen. There is thought to be tradeoff between disease resistance and production traits (Stear et al., 2001). Immune function is a life history trait that will trade off against other life history traits such as growth and reproduction (Colditz, 2008). Life history theory is often defined as a set of evolved physiological strategies and behaviors that influence fitness and the allocation of resources (Rauw, 2012). If resources are allocated towards an animal's immune function it reduces the resources available for other life history traits (Colditz, 2008). Animals that are allocating resources towards an immune response and experiencing a fever may see a loss in ADG as a result of resources being directed away from growth. However, not all animals allocate resources the same way. Animals selected for high production levels may allocate a greater amount of resources to production, leaving fewer resources for maintenance and immune function (Rauw, 2012).

SUMMARY

This thesis evaluated Nellore-Angus halfblood reciprocal F_2 and F_3 steers (n = 372) produced in the Texas A&M AgriLife Research McGregor Genomics project for weight and growth through different stages of life, including following a standardized bovine viral diarrhea virus (BVDV) challenge. There were no differences due to calf type for birth weight. The F_3 steers were lighter than all of the F_2 calf types at weaning, a year of age and 15 months of age. All of the F_2 steers were out of F_1 dams whereas the F_3 steers were out of F_2 dams. According to the dominance model a loss of heterozygosity is expected to occur between the F_1 and F_2 generations (Gregory et al., 1991) although SNP data do not support this assertion (Gill et al., 2009). These maternal effects may also be carrying over into postweaning weights (Meyer, 1991). The F_3 calves were also lighter than all the F_2 calf types during the health and feed trial.

The NAAN steers were the heaviest out of all the calf types at weaning weight, yearling weight and 15 months of age. Across the health and feeding trial weights, F_2 steers out of AN dams were 7 to 10 kg heavier than F_2 steers out of NA dams. These results are similar to the findings of Boenig (2011), which showed that F_2 calves out of Hereford-Brahman dams were heavier than F_2 calves out of Brahman-Hereford dams. Reciprocal differences in placental weight have been observed in interspecies mating of *Peromyscus* mice. (Vrana, 2007), and these differences have been speculated to result from genomic imprinting and possible X

chromosome involvement. Parent-of-origin effects have also been shown to control myofiber development (Xiang et al., 2003).

Similar patterns were observed for average daily gain across stages of development. From birth to weaning the F_3 steers had 0.10 to 0.13 kg/d lower ADG than the F_2 steers. However, across the 42-d health trial the F_3 steers' ADG was not significantly different from both types of F_2 steers out of NA dams. The F_2 steers out of AN dams gained slightly more per day than the F_2 steers out of NA dams. When the trial was broken down into three 14-d time periods, the differences in performance due to calf type became more obvious. During the first two weeks, immediately following exposure to the pathogen, all calf types had much lower average daily gain than in the following two time periods; in general, ADG was highest for all calf types in the second 2-week period, possibly as a result of compensatory gain. During the final two weeks of the trial, F_2 steers out of AN dams gained between 0.13 and 0.21 kg/d more than F_2 steers of NA dams.

The F_2 steers out of AN dams also ranked higher for monocyte counts than F_2 steers out of NA dams. Although there was no correlation between ADG during the BVDV health trial and monocyte counts, monocyte counts were significantly correlated (r between 0.18 and 0.13) to ADG from weaning to a year of age. The F_2 steers out of AN dams did gain between 0.1 and 0.2 kg more per d from weaning to a year of age than F_2 steers out of NA dams. Although there was not an inverse relationship observed between growth traits and monocyte counts, there may be an inverse relationship between animals that exhibited fever and pre-trial ADG.

Different patterns of relationship were present involving rectal temperature change after BVDV challenge and ADG at different stages among the different calf types. The NANA (r = -0.52, *P* = 0.003), F_3 and NAAN steers had negative correlations of rectal temperature change and ADG from d 0 to 14 post challenge. The rectal temperature change post-BVDV challenge was positively correlated with ADG from weaning to yearling weight for NANA (r = 0.62, *P* = 0.002) and ANNA (r = 0.28, *P* = 0.026) steers. Only ANAN steers had a relationship for preweaning ADG with rectal temperature change from BVDV challenge (r = 0.43, *P* = 0.046). In these cattle, the apparent trade-offs between growth and health responses appear inconsistent. The nature and interpretations of these reciprocal differences remain unclear and warrant additional research. Although it was not a component of this thesis, a genomic analysis of these animal may provide insight into the phenomena observed.

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