

GENETIC VARIANCE AND COVARIANCE COMPONENTS FOR FEED INTAKE,
AVERAGE DAILY GAIN, AND POSTWEANING GAIN AND INDICES TO IMPROVE
FEED EFFICIENCY IN GROWING BEEF CATTLE

by

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Abstract

Feed is the single most expensive cost related to beef cattle production. Currently a 70 d performance test is recommended for accurate calculation of efficiency. Previous research has suggested intake tests can be limited to 35 d. Objectives of this study were to estimate genetic parameters for growth and intake traits, compare two alternative indices for feed efficiency, and quantify the genetic response to selection for feed efficiency combining an intake test with two types of gain data. On-test average daily feed intake (ADFI), on-test average daily gain (ADG), and postweaning gain (PWG) records on 5,606 growing steers and heifers were obtained from the U.S. Meat Animal Research Center in Clay Center, NE. On-test ADFI and ADG data were collected from a minimum of 62 to 148 d testing days. Independent quadratic regressions were fitted for body weight on time, and on-test ADG was predicted from the resulting equations. PWG was calculated by subtracting adjusted 205-d weights from 365-d weights and dividing by 160. Genetic correlations were estimated using multiple trait animal mixed models with ADG, ADFI, and PWG for both sexes as dependent variables. The genetic correlations between ADG and PWG for both steers (0.81) and heifers (0.65) were strong. This indicates PWG is a strong proxy for ADG on-test and long test periods may not be necessary. Indices combining EBVs for ADFI and ADG and for ADFI and PWG were evaluated. For each index, the weighting of gain was arbitrarily set to 1.0 and the weighting for ADFI was the negative of the average of the intra-contemporary group ratio of mean gain divided by mean ADFI. Values were combined with EBV to compute two index values per animal. Pearson correlations for steers (0.96) and heifers (0.45) indicated a strong relationship for steers between the indices. Because more animals can be measured for intake, using PWG increases genetic progress of selection for feed efficiency by 15-17% per year. These findings support using PWG data in combination with ADFI to determine efficient animals, lessen costs, and increase annual feed efficiency genetic change.

Key words: beef cattle, feed efficiency, postweaning gain

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Chapter 1 - Literature Review

Importance of Feed Efficiency

Harris (1970) stated, “The primary goal of most livestock producers is, very simple, to make money.” The producer’s primary reason for purchasing certain breeding stock and the price he/she is willing to pay is based primarily on how the investment will affect his/her overall profit. Feed costs in beef production account for more than two-thirds of the cost of production in the U.S. cattle industry (Anderson et al., 2005). From 1990 to 2003, the cost of gain in the feed yard totaled \$261 per head. During the past 5 years, costs have risen to \$494 per head, nearly a 47% increase in the cost of gain (NCBA, 2014).

Compared to other meat animal species like pork or poultry, the inherent physiological differences of beef cattle contributes to lesser production efficiency. Lower reproductive rates of beef cattle also play a role in their inefficiencies. Beef cattle are a non-litter bearing species, which puts beef producers at a disadvantage compared to the swine producers. Not only do beef cattle have less progeny per year, but they also have longer gestation period, ranging from 280-291 days, compared to swine gestation, which ranges from 112-120 days. A major inefficiency of beef cattle is their feed conversion rate. Poultry, for example, have a conversion rate of 2:1, meaning that an animal eats 2 kg of feed per 1 kg of bodyweight gain; whereas, a beef animal’s conversion rate is greater than 6 kg of feed per 1 kg of bodyweight gain (Shike, 2012). Producers must recognize the importance of identifying animals genetically superior at converting feedstuffs into pounds of edible product in order to remain a competitive protein source for consumers (Hill, 2012). Although it is unreasonable to assume beef cattle will ever reach the

same degree of feed efficiency as monogastrics (Hill, 2012), animal scientists continue to focus efforts to attain more feed efficient beef animals.

Through the use of postweaning performance and individual intake tests, scientists are able to quantify feed efficiency traits that have been formerly overlooked. Previously, producers only had the ability to select for gain to increase feed efficiency within their herds due to technological inadequacies of individual measuring feed intake on pen-housed animals. Individually feeding animals twice a day to collect raw feed intake data was not efficient for commercially operated feeding enterprises of any size. However, collecting gain data and selecting animals based on high average daily gains was feasible, and gain data was readily used in the beef industry to increase the efficiency of livestock via selection for postweaning gain. Now, with the use of newly automated feeding technologies and advances in genomics, producers have the tools to select for both gain and feed intake. This change allows for increased accuracy when selecting for feed efficiency, allowing for greater genetic progress to occur.

Quantifying Feed Efficiency

Feed efficiency, as described by Koch et al. (1963), is the gain in body weight resulting from the consumption of a given amount of feed, or its inverse. It is a function of both body weight gain and feed consumption. Parameter estimates of components of feed efficiency, i.e. average daily feed intake (ADFI) and average daily gain (ADG), are described as moderately heritable; therefore, improving feed efficiency through genetic selection is possible (Koch et al., 1963). Precise data collection of ADFI and ADG is imperative in order to make predictions of feed efficiency, a trait that is not directly measurable. Once collected, ADFI and ADG are used to create feed efficiency phenotypes provided to producers as tools to select more efficient animals.

Gain Collection

Selection for increased growth rate has been practiced for more than 50 years because of its association with reduced cost of gain (Koch et al., 1963). Cost of gain is a highly valued economically relevant trait (ERT). It influences the cost of production per head or per unit of time. When weight gain increases, the cost of production decreases because of fewer days needed to reach market weight (Swiger et al., 1961). Studies have shown 10% greater gains during growing and finishing period improves profit by 18% for group fed cattle (Fox et al., 2001). Because of its importance to the industry, gain records should be collected with the highest degree of accuracy. Rate of weight gain requires at least two measurements to be taken at different times. The time periods between the recorded weights must be large enough for a significant weight change to take place. Change in body weights must be larger than the error of each individual measurement (Hill, 2012). On-test gain evaluations are derived differently in regards to performance test gains and postweaning gains reported by National Cattle Evaluation (NCE). Current Beef Improvement Federation (BIF) guidelines recommend at least a 70-d gain collection in order to derive phenotypes for feed efficiency. The recommended regression equation used to derive on-test ADG is as follows:

$$Y = \beta_0 + \beta_1x_1 + \beta_2x_1^2$$

where β_0 is initial body weight, β_1 is the linear term for the growth curve, or the amount of weight gained per d, and β_2 is the quadratic term denoting the curvature of the growth curve. The on-test ADG can be used by itself for selection strategies or for derivation for traits such as residual feed intake, residual average daily gains, and feed conversion ratio. However, on-test ADG is not required for routine evaluation of growth in National Cattle Evaluation (NCE). Currently, NCE requires producers to report 205-d and 365-d weights and dates for each animal.

This information is then used to determine postweaning gain. Because of the number of days and data points included in these two reported gains, different degrees of variation exist between on-test ADG and NCE postweaning gains. The amount of variation captured for performance test gains is less compared to variability of the entire postweaning gain interval because the number of testing days in a performance test is normally less than the 160 d postweaning interval. It is important to maximize the amount of variability captured during performance tests in order to accurately predict values for feed efficiency (Hill, 2012).

Feed Intake Collection

Feed intake is the second essential datum needed to capture the maximum amount of variability possible with feed efficiency models. It is imperative intake records are collected with high degrees of precision and accuracy. A 10% improvement in feed intake can increase potential profits by 43% (Fox et al., 2001). In order to represent feed intake as a single number (i.e. ADFI), it must be collected continuously throughout the testing period (Hill, 2012). In earlier decades, due to difficulties and inconsistencies of collection, feed intake was not recommended to be included as a predictor of feed efficiency (Koch, 1963). With recent advancements in automated feeding technologies, both gain and feed consumption are readily used as predictors for feed efficiency. The use of the Calan® Gate System (American Calan, Northwood, New Hampshire) is suitable for collecting intake data along with newer designs including GrowSafe® Systems, Ltd. (Airdrie, Alberta, Canada) and Insentec® Systems (Marknesse, Netherlands), which utilize electronic scales and radio frequency equipped identification ear tag to compile intake records. These systems must have capabilities to record individual animal identification which is unique yet compatible with other databases. A minimum 70-d test for feed intake collection is recommended by BIF to be incorporated into

NCE (BIF, 2010). A minimum three-generation pedigree must be on record to produce estimated progeny differences (EPD). Other essential information may consist of birth and weaning weights and dates, age of dam, and contemporary group information. Age on test is found to be another confounding factor on the accuracy of feed intake test results. Actual birth dates of animals entering the test must be recorded so age at the start of the test can be calculated (Hill, 2012).

For feed intake records to be included in genetic evaluation, it is recommended data be collected by the established protocols of BIF. Specific requirements are as follows. Intake data should be collected after weaning; weaning data collection is required before animals reach 260 d of age. Animals involved in feed intake tests should be older than 240 d of age when starting the test but younger than 390 d of age by completion. Acclimation periods should be incorporated into these testing windows. This period should consist of at least 21 d for animals to adapt to the testing facility and final test diets. Animals need to have start of test ages within 60 d of each other to be included into the same feed efficiency contemporary group. Test diets vary by animal type and gender, environment, feed availability and cost, and management. All different diet types can be adjusted to a common nutritional basis. However, all animals considered in one test should be fed the same diet. Feed is to be provided *ad libitum* with at least the required minimum bunk and pen space allowed (BIF, 2010).

Quality feed intake records are important to maintain a desirable level of accuracy. Electronic intake data recording systems have utilities to monitor these functions. System records for daily feed delivery should not differ by more than 5%. After individual feed intake records are taken, simple correlations among DMI, ADG, and body weight (BW) should also be checked

to test the validity of the data. Positive, moderate correlations must be derived or the data is deemed suspect, and may be removed from the data set (BIF, 2010).

Efficiency Phenotypes

Upon test completion, ADFI and ADG records are used as single trait selection parameters or manipulated to different develop selection tools. Phenotypes expressing feed efficiency include, but are not limited to, maintenance efficiency (ME), partial efficiency of growth (PEG), gross efficiency or feed conversion ratio (FCR), residual feed intake (RFI), and residual gain (RG). Three have predominated in the industry, namely RFI, FCR, and RG, where animals (Koch et al., 1963; Archer et al., 2004; Arthur, 2000).

Maintenance Efficiency

Ferrell and Jenkins (1985) described ME as the ratio of body weight to feed intake at zero body weight change. Feed energy maintenance requirements account for about 60-75% of the total energy requirements of individual breeding animals in a typical beef cattle system (Klosterman, 1972; Ferrell and Jenkins, 1985). Processes or functions comprising ME requirements include body temperature regulation, essential metabolic processes, and physical activity. Maintenance energy of an animal experiencing change in body composition and weight deviation during pregnancy or lactation is difficult to quantify (Koong et al., 1982). Although important to consider, maintenance efficiency lacks practicality, as it cannot be measured in growing animals. In order to obtain true measurements of ME, cattle must be held at a constant live weight for almost 2 years (Taylor et al., 1981). These measures are costly to collect and not economically viable, especially for a large population (Archer et al., 1999).

Partial Efficiency of Growth

A second phenotype to characterize feed efficiency is PEG. Partial efficiency of growth is defined as the total amount of feed used for growth after maintenance energy requirements are met. It is highly correlated with RFI as both incorporate feed intake data with ADG parameters derived from standard maintenance and growth measures. Generating PEG is nothing more than evaluating this simple ratio:

$$\text{Partial Efficiency Growth} = \text{ADG}/(\text{FI}-\text{Fm})$$

where *FI* dictates total feed intake and *Fm* represents the feed required for maintenance (Arthur, 2000). Due to the constraints on accurately measuring maintenance requirements of animals, this phenotype, like maintenance efficiency, is not feasibly applied to large groups (Archer et al., 1999).

Feed Conversion Ratio

Feed conversion ratio (FCR), or gross efficiency, is a well-known, simple phenotype to observe. It is the ratio of amount of feed consumed to the amount of BW gain over a set amount of time. Usually FCR is collected on a time-constant interval meaning growth and feed intake are measured between two set points on a line. Another alternative includes weight-constant intervals, described as the amount of feed required for growth from weight *a* to *b*. A third method, maturity-constant intervals, incorporates feed and weight gain measured from stages of maturity *a* to *b* (Archer et al., 1999). This ratio allows for the gathering of important information about performance of a particular set of animals. When FCR is collected this way, it provides little information about individual variation between animals, which is detrimental to the use of this parameter as a genetic prediction tool in NCE (Hill, 2012). Feed conversion, like so many ratio measures, is also highly correlated with other traits such as growth rate and maturity. These

high correlations with FCR make it difficult to detect whether the variation in feed efficiency is additional to or a byproduct of production levels or maturity patterns (Archer et al., 1999). This leads to a false sense of improvement of efficiency. This ratio is negatively correlated with postweaning ADG, yearling BW, mature size, and maintenance energy. Directly selecting on FCR increases genetic merit for growth but also increases mature size and maintenance requirements. This has an antagonistic effect on feed consumption, which does not translate into improvements in overall system efficiency. Because of its simplistic nature, FCR experiences desirable change by a decrease in feed intake or an increase in gain. A selection pressure on increased growth rates creates more favorable FCR measures, but true efficiency of the beef cattle system remains relatively unchanged (Koots et al, 1994b).

Residual Feed Intake

Residual feed intake (RFI), also referred to as net feed intake or net feed efficiency, assesses the difference between actual feed intake and predicted intake. Predicted intake is based on requirements for production and body weight maintenance (Koch et al., 1963; Kennedy et al., 1993). Koch et al. (1963) realized efficiency measures had to allow for adjustments in feed intake for cattle in various industry segments. For example, in growing animals growth energy is the major requirement, but in mature animals body weight maintenance is the major energy requirement. Individual feed intake can be expressed for an animal in a specific production scenario:

$$\text{Predicted Feed Intake} = b_M \times (BW)^{0.75} + b_P \times (\text{Amount of Production})$$

where b_M equals the amount of feed required per unit of metabolic body size, b_P is the amount of feed required per unit of production, BW is body weight (Nielsen et al., 2013). Predicted feed intake is then used to calculate RFI as follows:

$$\mathbf{RFI_i = Actual\ Feed\ Intake_i - Predicted\ Feed\ Intake_i.}$$

Koch et al. (1963) suggested partitioning feed intake into two components: 1) feed intake expected for a given level of production; and 2) the residual portion. Unlike FCR, RFI measures are phenotypically independent of both growth and mature size. Both factors allow for comparison of animals at different stages of production and energy requirements (Archer et al., 1999). A negative RFI value designates that an animal ate less than predicted, hence being more favorable. RFI is said to be phenotypically independent of production traits; however, it has been suggested the efficiency characteristic is not genetically independent of production (Kennedy et al., 1993). Kennedy et al. (1993) recommended using genetic (co)variances to calculate genotypic RFI. This ensures independence from production traits, reflecting the truer genetic variation between feed intake and production (Archer et al., 1999).

Much of the current research done on RFI has been focused primarily on the growing and feeding segment of the industry. Studies quantifying the genetic parameters of RFI estimate the trait to be moderately heritable, similar to the estimates of traditional growth traits (Koch et al., 1963; Arthur et al., 2001a,b; Schenkel et al., 2004). The economic impacts on the beef industry by incorporating RFI have been explored. Results indicated a 9% to 33% improvement in profit when an optimal number of bulls for feed intake were selected (Archer et al., 2004).

Residual Body Weight Gain

Residual body weight gain (RG) is also a derived difference to measure feed efficiency, but on a gain basis rather than intake. Initially proposed by Koch et al. (1963), this phenotype is the difference between actual and predicted daily BW gain. Greater or more positive RG values are more desirable (Crowley et al., 2010). The following model explains the RG calculation for growing animals (Berry and Pryce, 2014):

$$\mathbf{RG} = \mathbf{ADG} - (\mathbf{b}_1\mathbf{WT}^{0.75} + \mathbf{b}_2\mathbf{FI} + \mathbf{b}_3(\Delta)\mathbf{Fat} + \mathbf{b}_4\mathbf{WT}^{0.75}*\mathbf{Fat}).$$

ADG for this scenario was computed by regressing weight on time. Unlike RFI, RG places greater emphasis on gain rather than intake. Because of this, the most favorable RG cattle will have greater daily gains than the most favorable RFI cattle. However, the most favorable RFI cattle will eat less than the most favorable RG cattle (Crowley et al., 2010). Parameters like RFI and RG force producers to place emphasis on either input or output costs, which may not allow them to reach maximum profitability.

A recent push to predict phenotypes for cattle without intake records has rivaled other methods. Without feed intake records, marker-assisted selection must be exploited to detect efficient animals. The American Angus Association (AAA) launched an EPD for measuring feed efficiency in Angus cattle titled residual average daily gain (RADG). This EPD evaluates the difference between actual gain and predicted gain based on the animal's intake, body weight, and composition. Indicator traits used for this analysis include weaning weight, postweaning body weight gain, subcutaneous fat depth, and feed intake (MacNeil et al., 2011). With the use of genomics, trait markers for dry matter intake (DMI) are utilized for prediction of RG EPDs for animals lacking feed intake records (AAA, 2010). The trait is defined as a linear function of component EPDs including gain, feed intake, and fat; the model is as follows:

$$\mathbf{EPD}_{\mathbf{RADG}} = \mathbf{EPD}_{\mathbf{Gain}} - \mathbf{b}_1 * \mathbf{EPD}_{\mathbf{FI}} - \mathbf{b}_2 * \mathbf{EPD}_{\mathbf{FAT}} \text{ (MacNeil, 2010).}$$

Larger, more positive numbers are more desirable, as this means an animal gained more than was expected (MacNeil et al., 2011). Traits used to calculate RADG are moderately heritable ($h^2 = 0.31$ to 0.41) (Northcutt & Bowman, 2010). This approach is similar to the approach proposed by Kennedy et al. (1993) using RFI to select for feed efficient animals. Genetic improvement with the use of RADG is theoretically achievable for improvement of

feedlot animals. However, its high correlation to growth parameters may yield bigger cows with greater nutrient requirements.

Residual Intake and BW Gain

Research conducted on RFI and RG have raised concerns of their validity in determining the most efficient animals. With RFI, slow-growing animals consuming less but also gaining less will receive favorable RFI value. RG identifies high-gaining cattle, projecting less emphasis on the amount of feed consumed. A growing animal could receive a favorable RG value, gaining rapidly but eating substantially more than its contemporaries. Residual intake and BW gain (RIG) is an index trait combining RFI and RG still independent of BW (Berry and Crowley, 2012). This trait allows breeders to identify cattle of greater efficiency without overemphasizing either intake or gain traits, and without affecting mature cow size. Using RIG is equivalent to using raw intake and gain data directly in an index if appropriate weighting factors and correlation estimates are applied (Berry and Pryce, 2014).

Studies involving comparisons between RIG and RFI indicate slow-growing animals receiving high rankings on the RFI scale would not falsely excel in RIG rank. Consequently, superior RIG cattle ate less to achieve the same weight gain compared to superior RFI or RG cattle (Berry and Crowley, 2012). Combining RFI and RG in an index avoids the pseudo-rankings reported previously; however, to improve overall system efficiency one must instill economic weights into the index formulation to identify maximum profit (Archer et al., 1999). Continual efforts are being made in order to distinguish and supply the industry with the most accurate phenotypes to determine feed efficiency.

Optimal Postweaning Test Interval

Accurately measuring and predicting phenotypes for feed efficiency in growing animals is partly influenced by the number of days included in the postweaning test interval (Swiger et al., 1961; Koch et al., 1982). Genetic correlations among short- and long-day postweaning test intervals tend to be larger and more positive than either environmental or phenotypic correlations. This indicates genetic influences persist from one interval to the next and selection based on short intervals predicts long interval performance. Genetic correlations among test lengths tend to decrease as the number of days separating the interval increases (Koch et al., 1982).

Studies have indicated shorter postweaning tests do not have the same capabilities to capture the variation in gain and feed consumption as their longer counterparts (Archer et al., 1997). Determining the optimum test duration for gain and intake increases efficiency of these tests to maintaining desirable amounts of accuracy. Shortening postweaning test intervals also allows for decreased evaluation costs as well as the opportunity to reduce excessive fattening of breeding stock (Swiger et al., 1961). With collection costs for feed intake valued approximately at \$100 per head (Fox et al., 2001), shortening intervals could cheapen testing costs. Shorter tests provide the opportunity of increased usage of equipment, allowing for those costs to be spread over a greater number of animals. Calculations based on feed intake measurements at the Agricultural Research Centre, Trangie, NSW, propose shortening the testing interval by one week would save roughly \$35 (AUD) per head (Archer et al., 1999). A shorter test not only provides for the opportunity of decreased costs but also accelerates genetic improvement of feed efficiency. The latter occurs because a greater number of animals can be tested in the same amount of time, which, in turn, would increase selection intensity driving the rate of genetic change in a positive direction.

Performance gain tests have been dramatically shortened to the current 70-d standard performance tests recommended by the BIF Guidelines. Studies still indicate the accuracy for using gain as a predictor of efficiency increases when the full 160-d collection period is implemented (Swiger et al., 1961). Gain and feed efficiency are highly correlated ($r=0.64$; Koch et al., 1963), hence predicting feed efficiency is more dependent on ADG than ADFI. For this reason, limiting the amount of accuracy lost for gain is a primary goal. Swiger and others (1961) promoted daily intake and gain evaluations of 168 d. Another study in the same year reported the interval for performance testing beef bulls could be shortened from 140 d to 112 d without severe compromise of accuracy (Brown, et al., 1991). Archer et al. (1997) declared test day lengths could be shortened from 119 d to a 35 and 70 d test for ADFI and ADG, respectively. In 2006, Wang and others presented a study again supporting a 35-d intake test and also suggested shortening ADG tests to a 63-d window. Numerous studies (Archer et al., 1997; Wang et al., 2006) involving the variance components, heritability, and correlation estimates of ADFI in beef cattle support the validity of a shortened intake test of 35 d. On the contrary, those same studies conclude that a gain test can only be shortened to a minimum of 70 d, with only one study supporting a shorter 63-d test without a severe loss in accuracy. Although shortening these tests would economically benefit producers, effects of the shortened test- day intervals for both genetic and phenotypic parameters must be considered.

Variance Components

Variance components, or the measure of variability in the population due to genetic and residual variation, tend to differ when test intervals are shortened; therefore, it is important to examine how much of the variation is captured within a shortened test interval. Several studies have compared genetic and environmental variance components for both ADFI and ADG.

Various days on test were examined to determine whether adding additional data to the assessment was effective in reducing the amount of unexplained environmental variation of the traits (Koch et al., 1982; Archer et al., 1997; Wang et al., 2006). Genetic effects tended to account for a larger fraction of the variation in traits with longer testing intervals (Swiger et al., 1961; Koch et al., 1982). In 1982, Koch et al. noticed an increasing linear trend in genetic variation with increased number of days on test for gain. Shorter gain tests with smaller increments between measurements have been studied and similar patterns of increasing genetic and decreasing residual variances have been realized with longer testing. Archer et al. (1997) reported residual variances of ADG decreased from 0.071 to 0.018 from 28 to 70 d. After d 70, slight decreases in residual variances were recorded. Daily feed intake achieved notable decreases in residual variation from 7 to 35 d. Residual variance decreased from 0.75 to 0.45 without any substantial decreases after d 35. A study in 2006 reported variance reduction fluctuated throughout a 91-d trial, providing an unclear trend for ADG. However, DMI followed a similar pattern to the previously mentioned study, showing a dramatic downward reduction in phenotypic variance from 7 to 35 d (Wang et al., 2006). These reports on variance components support the idea that reducing test day intervals for feed intake can be done without severely affecting the amount of genetic variation explained.

Heritability is the proportion of the difference in performance that is attributed to the differences in breeding value, or additive genetic variance for that trait. A greater heritability indicates animal performance is a good indicator of breeding value for a trait. Heritability is as follows: $h^2 = \hat{\sigma}_a^2 / \hat{\sigma}_p^2$, where $\hat{\sigma}_a^2$ represents the estimated additive genetic variance and $\hat{\sigma}_p^2$ indicates the estimated phenotypic variance in the model. Most research has concluded measures

of feed efficiency, feed intake, and growth traits, including average daily gain (Koch et al., 1963; Arthur et al., 2001; Nkrumah et al., 2007; & Rolfe et al., 2011) are moderately heritable.

Studies with varying test lengths have reported differences in heritability estimates for both ADG and ADFI. For instance, in 1963, Koch et al. derived heritability estimates for a 168-d interval of 0.65 for on-test gains and 0.62 for on-test feed intake. Specific studies have been conducted to provide information on the differences in accuracy among test period lengths measuring for growth and consumption. All studies have found that with increased length of the test period, average heritability estimates also increase. More importantly, these estimates increase at a decreasing rate (Koch et al., 1982). Koch and others reported the heritability of gain from seven successive 28-d periods. Heritability averages increased from 0.16 to 0.55 as the interval increased from 28 to 224 d on test. When using regressions as an alternative to NCE daily gain no differences in heritability estimates were observed between the two methods (Koch et al., 1982). This was different than what Mavrogenis et al. (1978) reported in earlier studies when conducting postweaning performance tests in growing bulls. Data suggested regressions ($h^2 = 0.41$) were much more heritable for gain than were reported for NCE PWG ($h^2 = 0.27$). Mavrogenis and others also reported a heritability estimate for ADFI of 0.44 during this postweaning test. Archer et al. (1997) divided a 119-d test into 17 successive 7-d periods. Growth measurements were modeled using linear regressions, and consumption was calculated by dividing the amount of energy provided by the number of days on test. Heritability estimates for ADG increased from 28 d ($h^2 = 0.13$) to 70 d until topping out at 0.35. The maximum average daily feed intake heritability estimate was 0.65 at 35 d. After day 70 and 35, no further gains in heritability estimates for ADG and ADFI, respectively, were seen with longer tests (Archer et al., 1997). In all cases, heritability estimates ranged from 0.16 to 0.65 for either ADG or ADFI.

Correlations

Genetic correlation measures between short and long testing intervals have also been estimated. In general, correlations are compared among shortened test day intervals and one longer “standard” test day interval to measure accuracy loss due to shortened test periods. In 1991, Brown and others reported Spearman rank correlations between an 84-d and 112-d test for ADG and ADFI of 0.88 and 0.96, respectively. Archer et al. (1997) compared several shorter intervals to a longer 119-d interval. Results indicated only minor animal re-rankings occurring when a 35-d test for feed intake and a 70-d test for growth rate were compared to a 119-d test. Genetic and phenotypic correlations for feed intake were 0.74 and 0.90 between 35 and 119-d tests, respectively. Genetic and phenotypic correlations were 0.78 and 0.99 for ADG between tests of 70 and 119 d. Wang et al. (2006) compared shortened test day periods to a 91-d standard reporting both Spearman Rank and Pearson genetic correlations. Correlation estimates between a 35- and 91-d ADFI test, were 0.929 (Pearson) and 0.931 (Spearman). A 63-d test when compared to a 91-d test for ADG reported estimates of 0.898 (Pearson) and 0.872 (Spearman). These results concluded shorter intervals could be implemented without severe loss in accuracy. Similar results have been found in other species, namely growing pigs. The industry standard for performance testing growing pigs is 120 to 140 d. A study by Arthur et al. (2008) in pigs indicated performance tests could be shortened to 28 d for ADFI and 35 d for ADG with phenotypic correlations of 0.91 compared with the 119-d test.

Breed Effects

Genetic improvement of beef cattle is often accomplished through crossbreeding, selection within a breed, or the combination of these two factors (Hill, 2012). Knowing breed ranks for feed efficiency would be an advantage for many commercial cattlemen. Being able to

distinguish the differences in efficiency allows producers to be able to make economically sound decisions regarding these performance characteristics. Feed efficiency model accuracy is highly dependent on precise measures of breed performance for these traits (Chewning et al., 1990). Studies have shown significant breed differences for growth rates, feed efficiency, and feed utilization in growing beef animals do exist (Smith et al., 1976; Cundiff et al., 1981; Chewning et al., 1990; Moore et al., 2005). Genetic variation and heritability measures have also been examined within and between breeds.

Improving feed efficiency could be as simple as switching from a less efficient to a more efficient breed if feed efficiency is the sole criterion to be considered. Studies testing phenotypic and genetic parameters have resulted in identifying breed differences in genetic merit and heritability of feed efficiency. Arthur et al. (2001a) reported heritability estimates of 0.34 for ADG, 0.48 for FI and 0.39 for RFI for Angus cattle. Similar results were reported in Charolais cattle (Arthur et al., 2001b) with heritability estimates for ADG, ADFI, and RFI of 0.28, 0.39, and 0.39, respectively. Other studies have evaluated these three traits on mixed or crossbred populations. A Canadian composite population in 2007 denoted heritability estimate of 0.54 for DMI 0.21 for RFI (Nkrumah et al., 2007). In 2009, some of the highest heritability estimates (DMI = 0.48, ADG = 0.21, RFI = 0.48) reported in purebred cattle were of Brangus cattle (Lancaster et al., 2009). A mixed U.S. population performance test reported heritability measures for DMI at 0.40, ADG at 0.26, and RFI at 0.52 (Rolfe et al., 2011).

Studies have examined animal populations involving several different breeds. Gregory et al. (1966) evaluated breed effects for a population of purebred Hereford, Angus, and Shorthorn cattle along with their reciprocal crosses. Results of this study indicated breed differences existed for ADG and total digestible nutrients (TDN) consumed per unit of gain. Another approach to

evaluate breed effects is to analyze efficiency based on varying end points. Smith et al. (1976) and Cundiff et al. (1981) looked for breed comparisons for postweaning growth and feed efficiency of steers for three different endpoints: age-constant, weight-constant, and fat-constant intervals. Gregory et al. (1994) evaluated gain efficiency on time-constant, gain-constant, carcass weight-constant, and retail product weight-constant intervals. Breed differences were significant for all endpoints of the three different studies; however, breed ranks varied depending on the endpoint being considered. For example, breeds with smaller weights to maintain seemed more efficient on time-constant intervals, whereas breeds with the higher rates of gain were more efficient on the gain-constant periods (Gregory et al., 1994). Some studies reveal that breed differences exist for different feed efficiency phenotypes with some consistency in breed ranks among studies. Schenkel et al. (2004) evaluated six different breeds, including Charolais, Limousin, Blonde d' Aquitaine, Simmental, Angus, and Hereford. Crowley et al. (2010) evaluated five different breeds: Charolais, Limousin, Simmental, Angus, and Hereford. The results from these studies indicated differences among *Bos taurus* breeds were measurable. Similar breeds were used in each study and identifiable patterns among breeds arose. Charolais and Limousin cattle had consistently smaller RFI values than Angus and Hereford cattle in both studies (Schenkel et al., 2004; Crowley et al., 2010). In 2013, breed differences between Angus and Simmental cattle were quantified. Simmental cattle reported more favorable RFI values in comparison to Angus cattle (Retallick et al., 2013). These studies demonstrated genetic variation among breeds exists for feed efficiency traits, allowing us to improve profitability of the production system with breed selection.

Heterosis Effects

Knowing breed differences allows for the creation of crossbreeding programs to take advantage of breed complementarity. Hybrid vigor or heterosis is another advantage of crossbreeding. Heterosis is a measure of the superior performance of a crossbred relative to the average performance of the purebred parents involved in the cross. Crossbred progeny from mating breeds more genetically unrelated generally have a greater degree of heterozygosity, resulting in greater performance. Specific crosses, sire or dam breeds, and breed fractions involved in crosses affect the level of heterosis.

Growth traits generally have moderate levels of heterosis. Gregory et al. (1966) found heterosis had significant effects on both growth rate and feed efficiency, measured as TDN consumed per unit of gain, when studied on weight-constant intervals. These findings affirmed that more genetically distant animals tended to have greater increases in both growth rate and feed efficiency due to heterosis, as larger effects on performance were observed for Hereford-Angus and Hereford-Shorthorn crosses than Angus-Shorthorn crosses (Gregory et al., 1966). Given the strong correlation between gain and efficiency ($r = 0.64$), this increase in feed efficiency was likely due to increased gains (Koch, 1963). Smith et al. (1976) evaluated heterosis effects on Hereford-Angus crosses for weight-constant intervals along with age- and fat-constant intervals. Unlike the study by Gregory et al. (1968), data suggested no significant heterosis effects on feed intake for any interval were observed. A similar study echoed Smith et al. (1976) reporting Hereford-Angus crosses did not gain significantly faster than either purebred Hereford or Angus cattle over time- or weight-constant intervals (Cundiff et al., 1981). A study examining the composite populations (MARC I, MARC II, and MARC III) at the Meat Animal Research Center in Clay Center, Nebraska, an inconsistent effect of heterosis and retained heterosis, or the amount of hybrid vigor remaining in the later generations of crossbred animals,

of the various populations. While the retained heterosis effects were near zero in the MARC I, MARC II and MARC III heterosis effects fluctuated among the three composite populations. Larger initial on-test weights of the MARC I and MARC III composites resulted in less efficient animals compared to parental breeds on time-constant intervals. The MARC II population observed greater gain efficiencies on gain-constant intervals because of heterosis. For fat-constant intervals, MARC II animals tended to be more efficient, whereas, MARC I and MARC III decreased slightly compared to parental breeds. Heavier initial weights led to increased maintenance requirements, making MARC I and MARC III animals less efficient overall (Gregory et al., 1994). A study involving 581 Angus, Brahman, and Angus-Brahman calves found heterosis tended to improve feed efficiency for RFI. However, heterosis was not a statistically significant factor in changing either RFI or FCR (Elzo et al., 2009). Rolfe et al. (2011) again found varying outcomes of heterosis effects on assorted measurements. Even though heterosis did not significantly affect ADG or G:F, it did contribute to larger, less desirable DMI and RFI values. A study examining Angus, Simmental, and Angus-Simmental cross cattle found DMI and RFI was not affected by individual heterosis, but individual heterosis desirably increased G:F and residual gain (Retallick et al., 2013). The fluctuating conclusions suggest modest improvement of feed efficiency parameters due to heterozygosity at best. To date, it is likely none of these studies were large enough to confidently estimate the effects of heterosis on feed efficiency.

Genetic Evaluation of Feed Efficiency

Creating separate EPD for intake and growth parameters makes it difficult to identify favorable animals and possibly detrimental to long term selection. Intake and growth traits are antagonistic. Pressure placed on one trait will negatively affect the other, hindering acceleration

of system efficiency or (Archer et al., 1999). Placing heavy selection pressure on either component trait could also negatively affect other highly correlated traits with either intake or gain. Various methods and their efficacies have been explored to determine the best selection technique for feed efficiency. Single trait selection on gain is the most simplistic approach. Gain is selected because it is easier and cheaper to measure, along with being more heritable than intake. Additionally, selection on the phenotypic ratio of G:F or F:G or RFI and RG has been used to increase feed efficiency. Selecting on raw ratios or RFI and RG does not allow for differing economic weights to be placed on component traits; therefore, ranks of animals enrolled in the process would not be the same with or without the addition of economic weights. Ratios can also change by increasing or decreasing the numerator or denominator, possibly inflating relative change in feed efficiency superficially. An alternative and presumably more efficient methodology for analyzing feed efficiency includes selecting parameters based on the linear approximation of the efficiency ratio, namely a linear index (Lin and Aggrey, 2013). Both restricted and unrestricted linear indices have been evaluated. This would provide the ability to hold one component trait constant, in this case intake, whereas the other (gain) is left unhampered. However, data indicates using a restricted linear index does not allow maximize profit from increase weight sold and/or decreased feed fed (Lin, 1980).

Selection Index

Selection index theory is a method to evaluate livestock for several important traits simultaneously. It is a technology used to maximize genetic potential for a certain objective, for example profitability (Hazel, 1943). First developed in the 1930s to estimate breeding values, selection indices were used to combine information sources for genetic prediction to make a linear prediction of breeding value. Sources of information include: 1) the animal's own

performance record; 2) the animal's pedigree; and 3) progeny data. Properties of a selection index include: 1) minimizing the average square prediction error; 2) maximizing the correlation between the true breeding value and the index; and 3) maximizing probabilities of correctly ranking pairs of animals on their breeding values. Observations on measured traits, including breeding values can be combined into a selection index written as:

$$\mathbf{I} = \mathbf{b}_1(\mathbf{y}_1 - \boldsymbol{\mu}_1) + \mathbf{b}_2(\mathbf{y}_2 - \boldsymbol{\mu}_2) + \mathbf{b}_3(\mathbf{y}_3 - \boldsymbol{\mu}_3)$$

where \mathbf{I} denotes the index and \mathbf{b}_1 , \mathbf{b}_2 , and \mathbf{b}_3 represent weighting factors or regression coefficients (Mrode, 2013).

A selection index can also be used to combine multiple traits with their relative economic values to predict an animal's aggregate breeding value (Henderson, 1963). Hazel and Lush (1943) found, with properly weighted traits, an index is a more efficient selection tool to reach a breeding objective than single-trait selection or selecting several traits with independent culling levels. Phenotypic indices allow for selection of more than one trait of interest at a time for within herd evaluation; however, it is unsuitable for NCE. Using index theory in combination with multiple trait NCE EBV models provides a more robust measure (MacNeil et al., 1997). This approach allows for selection of both intake and gain traits at once with appropriate economic weights applied. Thus far, most efficiency measurements do not take this approach and arbitrarily place more emphasis on one element to describe feed efficiency (i.e. RFI or RG).

In order to incorporate linear approximation in the evaluation of feed efficiency, the genetic ratio of weight gain to feed consumption must be transformed to a linear scale (Lin and Aggrey, 2013). Gunsett (1984) evaluated improving ratio traits using index selection. The study indicated that a linear index places a predetermined amount of selection pressure on the traits of interest. Gunsett's methodology estimates that the amount of genetic change of each component

trait increased more rapidly with index selection compared to direct ratio selection. Using this information, a linear index maximizing the correlation between the index and the genotype was created for specific ratios (Gunsett, 1984).

Koch et al. (1963) took an early lead on comparing methodologies to determine linear indices and making improvements on feed efficiency. Early findings of high correlations between growth and feed efficiency and the cost of collecting feed intake led to the inclusion of only growth data into feed efficiency phenotypes (Koch et al., 1963). Since this time, the need to include feed intake measures in selection indices has been more evident (MacNeil et al., 2011) primarily because of the increased feed cost and easier intake measurement systems. Breeding values estimating residual gain and residual feed intake are advocated to improve feed efficiency. However, restricting selection of efficiency to intake or gain will only allow suboptimal economic results of the system (MacNeil et al., 2013) Using the linear index actually increases overall response of feed efficiency indicating a greater genetic progress (Gunsett, 1984; Lin, 1980; Lin & Aggrey, 2013). Developing a well-weighted linear index combining breeding values and relative economic values for both gain and intake appears to be the most plausible way to select animal that are genetically optimal for feed efficiency.

Economics & Weighting Factors

Economics plays a pivotal role in projecting the efficiency of any system. Many of the approaches to define feed efficiency are biologically based. An economic index providing a clear economic target to increase efficiency is preferable to a biological index (Archer et al., 1999). When constructing an economic selection index, information on phenotypic constants including standard deviations of each trait, phenotypic correlations between pairs of traits, and phenotypic correlations between traits of relatives is needed. Genetic constants including heritability

estimates and genetic correlations are also necessary along with the relative economic values of each trait (Hazel, 1943). The issue with any selection index, economic or biologic, is predicting weighting factors resulting in the maximum economic or biologic gain of the index (Lin, 1980).

Weighting factors are the combination of all three parts. These coefficients are difficult to derive as relative economic values can fluctuate by environment and breeding objective. Proper weights are crucial to reach maximum levels of genetic response (Mrode, 2013). The goal is to derive selection index coefficients, or weight factors, to achieve two things: 1) maximize response to aggregate genotype; and 2) create an unbiased predictor of aggregate genotype such that the true value, on average, is no more likely to be greater or lesser than the selection index (Lin, 1980).

Several industries have adopted this technology to improve the genetic merit of animal populations. The USDA produced the first economic selection index, net merit, in 1971 for the dairy industry (VanRaden, 2005). Resistance to selection indices in beef industry persisted (Garrick and Golden, 2009) until 2010 when the American Simmental Association launched the all-purpose index followed up by the terminal index. Other breed associations, including the American Angus Association, American Hereford Association, American Simmental Association, Red Angus Association of American, American Gelbvieh Association, along with others have since adopted the idea.

Conclusions

Feed efficiency is an important characteristic for producers to take into account as it directly affects their bottom line through both costs and income. Research has concluded that feed efficiency parameters are moderately heritable. Much work has been done to derive phenotypes to be implemented into NCE. Indices weighted by economical values are likely the

most effective strategy. Breed associations and other organizations could incorporate selection of feed efficiency with indices and diversified testing strategies to accelerate the genetic change of feed efficiency per year.

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Chapter 2 - Genetic Variance and Covariance Components for Feed Intake, Average Daily Gain, and Postweaning Gain in Growing Beef Cattle

Introduction

Feed efficiency is an important attribute to consider for all facets of the beef industry. It is imperative that producers take a judicious approach when including this trait into breeding goals. Animal feed is a major input cost in most livestock operations, but measuring individual

feed intake on animals is difficult and expensive. Because of its arduous nature, most systems have focused on the genetic potential of output traits to increase production efficiency; however, recent improvements and investments in feed intake recording systems have increased the number of animals tested (Arthur et al., 2014). Both gain and intake records combined allow for maximum genetic progress for feed efficiency. Feed efficiency phenotypes including residual feed intake (RFI), feed conversion ratio (FCR), and residual average daily gain (RADG) have been proposed as selection criteria (Koch et al., 1963; Archer et al., 1999; MacNeil, 2011). These phenotypes demand both gain and intake records be observed. Using electronic intake monitoring systems like the GrowSafe® System or Insentec® Systems improves the efficacy of collecting these records; however, the expense of measuring intake still burdens the industry.

Because of these costs, scientists have worked to pinpoint optimal test durations for collecting both weight gain and feed intake records. Gain collection limits the degree to which these tests can be reduced (Archer et al., 1999; Wang et al., 2006; Arthur et al., 2008). A key study (Archer et al., 1997) recommended minimum test duration of 70 d with a 21 d warm up period. The same study recommended a 35 d test period for intake; however, accurately testing for gain in this shorter interval is not viable. A second study by Wang and others (2006) also supported testing intake over a 35 d interval. Seedstock producers in all the major U.S. beef breeds already routinely collect weight data at 205 and 365 days of age for various beef breed improvement programs offered by breed associations for National Cattle Evaluations (NCE). This data is then used to derive postweaning gain. The objective of this study was to estimate the genetic parameters of postweaning gain as calculated by NCE (PWG), on-test average daily feed intake (ADFI) and on-test average daily gain (ADG), determine correlations between PWG, ADG, and ADFI, and quantify breed effects of PWG, ADFI, and ADG.

Materials & Methods

Animal Populations and Management

Data on 5,606 growing steers and heifers for PWG, ADFI and ADG were obtained from the U.S. Meat Animal Research Center (USMARC), Clay Center, Nebraska, on cattle born from 2003 to 2012. Animal procedures were approved by IACUC at USMARC in accordance with FASS (2010) guidelines. A previous study by Rolfe et al. (2011) explored the genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and the opportunity to select on these traits. The calves, born from 2003 to 2007 and reported on in the 2011 study, were included as observations in the current study to improve estimation of variance components. Briefly, these animals were designated as F_1^2 progeny. The F_1^2 calves were produced with matings established through the USMARC Germplasm Evaluation Project (GPE). In Cycle VII of the GPE, the F_1 animals were produced. Cycle VII is comprised of Angus (AN), Hereford (HH) and composite MARC III [1/4 AN, 1/4 HH, 1/4 Pinzgauer (PZ), and 1/4 Red Poll (RP)] cows mated by artificial insemination to purebred AN, HH, Red Angus (AR), Charolais (CH), Gelbvieh (GV), Simmental (SM) and Limousin (LM) sires to produce F_1 progeny. The F_1 females born in 1999, 2000 and 2001 along with 2001 F_1 males were kept for breeding. These animals were mated in multiple-sire pastures to produce 2-, 3-, and 4-breed cross progeny namely F_1^2 progeny. More recent GPE generations from 2008 to 2012 were produced from continuous sampling from seven of the breeds involved in Cycle VII as well as several additional breeds: [Beefmaster (BM), Braunvieh (BV), Brahman (BR), Brangus (BN), Chiangus (CI), Maine-Anjou (MA), Salers (SA), Santa Gertrudis (SG), Shorthorn (SH), South Devon (DS) and Tarentaise (TA)]. Purebred AI sires were mated to purebred or crossbred dams (most from previous GPE cycles) resulting in purebred and crossbred steers and heifers. All sires selected to

be included in the germplasm evaluation were introduced through AI. Sires sampled had high accuracy EPD, based on Beef Improvement Federation (BIF) guidelines, and represented heavily used sires in the U.S. beef industry. Progeny from AI sires were preferentially assigned to the feed intake project.

Only spring-born steer records were collected for years 2003 and 2004 of the current study. Both spring-born steer and heifer records were included for years 2005 and 2006. From 2007 on, both spring- and fall-born steers and heifers were evaluated for this study. Male calves were castrated within 24 h after birth. Calves born from 2003-2007 were weaned at approximately 165 d of age, whereas calves from later generations were weaned at approximately 150 d of age. Age at weaning varied amongst years because of differing environmental conditions. Once weaned, heifers received a low concentrate, high roughage diet appropriate for developing heifers for breeding purposes. Steers were managed and fed for slaughter receiving a high-concentrate finishing diet.

Data Collection and Editing

Individual feed intake records on F_1^2 calves, born from 2003 to 2007 as described in Rolfe et al. (2011), were acquired using the Calan® Broadbent Feeding Systems (American-Calán-Broadbent, Northwood, NH, USA). Animals were trained on step-up diets then placed in pens of 4 or 8 animals equipped with Calan® gates. Animals were fed at 0800 h and given *ad libitum* access to feed. Feed intake records on calves born from 2008 to 2012 as a result of continuous sampling matings from the MARC population were collected using an Insentec® System (Marknesse, The Netherlands). The variation between the two separate feeding systems was accounted for through a feed management code built into respected contemporary groups.

Dry matter intake (DMI) records were collected for the entire feeding period, ranging from a minimum of 62 d to a maximum of 148 d. ADFI is total DMI divided by the number of days included in the test. Individual quadratic regressions were fitted for body weight on time. On-test ADG was then derived as the predicted final weight minus the predicted initial weight divided by the days on trial. Weaning and yearling weights were adjusted to a common age and age of dam for each animal. Postweaning gain (PWG) was calculated by subtracting 205-adjusted weaning weight from 365-adjusted yearling weight, then dividing by 160.

Data was edited by examining trends of on-test weights and disease records to remove any outliers. A four-generation pedigree containing 9,211 animals was used for data analysis. Breed origins of 27 different breed groups were fit as covariates in subsequent models. There were 18 different AI breed groups were fitted. In addition, 9 commercial dam breeds including AN, HH, SM, CH, Red Angus x Simmental composite (RS), Bonsmarra (BS), Romosinuano (RO), MARC II and MARC III composite populations were fitted as model covariates. Two separate contemporary groups for on-test data (ADG and ADFI) and PWG were defined based on recommendations given by BIF Guidelines (2010). The on-test contemporary group was defined as birth location, year-season, on-test date, off-test date and feeding management code. The PWG contemporary group was defined as birth location, year-season, weaning date and yearling weight date.

Statistical Analysis

Data was analyzed using multiple trait animal models with contemporary groups fit as fixed effects; age on test (AOT), age of dam (AOD), percent direct heterosis (expected heterozygosity), percent maternal heterosis and breed origin were fit as covariates in the models. Age of dam was fit as a covariate based on established BIF Guidelines (2010). Univariate and

bivariate animal models for ADFI, ADFI, and PWG or a combination of these traits as dependent variables were constructed to estimate starting values for larger subsequent models. Sexes (heifers, steers) were investigated separately to quantify the differences in the correlations between on-test ADG and ADFI and PWG. A tri-variate model for both steers and heifers including ADFI, PWG and ADG was configured using starting parameters from the bivariate models. The resulting estimated variance parameters from the tri-variate models were then used as starting parameters for the following six-trait model.

A six-trait animal model was derived to include all 3 phenotypic parameters (ADG, ADFI, PWG) for both sexes to be used as dependent variables. This allowed comparisons among steer PWG, ADFI, and ADG (SPWG, SADFI and SADG, respectively), and heifer PWG, ADFI and ADG (HPWG, HADFI and HADG, respectively). Random, fixed and covariate effects for this multiple trait model were identical to those involved in the bivariate animal model. For each of the six dependent variables, the mixed model equation can be expressed in the following form:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \\ \mathbf{y}_4 \\ \mathbf{y}_5 \\ \mathbf{y}_6 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1\boldsymbol{\beta}_1 \\ \mathbf{X}_2\boldsymbol{\beta}_2 \\ \mathbf{X}_3\boldsymbol{\beta}_3 \\ \mathbf{X}_4\boldsymbol{\beta}_4 \\ \mathbf{X}_5\boldsymbol{\beta}_5 \\ \mathbf{X}_6\boldsymbol{\beta}_6 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1\boldsymbol{\mu}_1 \\ \mathbf{Z}_2\boldsymbol{\mu}_2 \\ \mathbf{Z}_3\boldsymbol{\mu}_3 \\ \mathbf{Z}_4\boldsymbol{\mu}_4 \\ \mathbf{Z}_5\boldsymbol{\mu}_5 \\ \mathbf{Z}_6\boldsymbol{\mu}_6 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \\ \mathbf{e}_4 \\ \mathbf{e}_5 \\ \mathbf{e}_6 \end{bmatrix}$$

where \mathbf{y}_i was the vector of n_i observations for each trait (HPWG, HADG, HADFI, SPWG, SADG and SADFI). \mathbf{X}_i was the incidence matrix relating observations to the levels of fixed effects. \mathbf{Z}_i was an incidence matrix relating observations to additive genetic effects trait i , respectively. In addition, $\boldsymbol{\beta}_i$ was the vector of fixed effects, including feed efficiency and yearling contemporary groups. Finally, $\boldsymbol{\mu}_i$ was the vector of random additive genetic effects and permanent environmental effects and \mathbf{e}_i was the vector of random residuals. Matrix \mathbf{A} is the

numerator relationship matrix quantified through pedigree relationships. The variance structure for the animal effects was as follows:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \\ y_6 \end{bmatrix} = \mathbf{A} \begin{bmatrix} \sigma_{a1}^2 & & & & & \\ \sigma_{a1,a2} & \sigma_{a2}^2 & & & & \\ \sigma_{a1,a3} & \sigma_{a2,a3} & \sigma_{a3}^2 & & & \\ \sigma_{a1,a4} & \sigma_{a2,a4} & \sigma_{a3,a4} & \sigma_{a4}^2 & & \\ \sigma_{a1,a5} & \sigma_{a2,a5} & \sigma_{a3,a5} & \sigma_{a4,a5} & \sigma_{a5}^2 & \\ \sigma_{a1,a6} & \sigma_{a2,a6} & \sigma_{a3,a6} & \sigma_{a4,a6} & \sigma_{a5,a6} & \sigma_{a6}^2 \end{bmatrix}$$

The variance structure for the residual effects was as follows:

$$\begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \\ e_6 \end{bmatrix} = \mathbf{I} \begin{bmatrix} \sigma_{e1}^2 & & & & & \\ \sigma_{e1,e2} & \sigma_{e2}^2 & & & & \\ \sigma_{e1,e3} & \sigma_{e2,e3} & \sigma_{e3}^2 & & & \\ 0 & 0 & 0 & \sigma_{e4}^2 & & \\ 0 & 0 & 0 & \sigma_{e4,e5} & \sigma_{e5}^2 & \\ 0 & 0 & 0 & \sigma_{e4,e6} & \sigma_{e5,e6} & \sigma_{e6}^2 \end{bmatrix}$$

Error (co)variances between SPWG and HPWG, SADFI and HADFI, SADG and HADG, SPWG and HADFI, SPWG and HADG, HPWG and SADG, HPWG and SADFI, SADG and HADFI, and SADFI and HADG were fixed as 0 because no animal had observations for those combinations of traits. Variance parameters were estimated using ASREML (Ver 3.0, VSN International, Ltd., Hemel Hempstead, UK). Breed differences for the 18 AI sire breeds were estimated and expressed as contrasts among all 18 breed solutions for the 6 genetic parameters.

Results and Discussion

Descriptive statistics are provided in Table 2.1. The data set contained a greater number of steer versus heifer observations for all traits. All individuals had recorded measures for on-test ADFI and ADG, but a few had missing observations for PWG. Steers had higher average ADFI,

ADG and PWG compared to heifers. These higher average means for all three traits could be associated with the higher energy diet steers received throughout the trial period.

Variance components for steer and heifer ADFI, ADG, and PWG are shown in Table 2.2. All residual covariances between steer and heifer traits were set to zero. Heritability estimates along with genetic correlations are presented in Table 2.3. These estimates confirm that the genetic antagonism between growth and feed intake can be broken supporting selection for increased gain and decreased intake is viable, and genetic improvement of feed efficiency is feasible. On-test ADFI and PWG for both steers and heifers were moderately to highly heritable in these data. Estimates for on-test ADG for both sexes were lowly heritable in these data, which is dissimilar to estimates reported in previous literature. Nkrumah et al. (2007) reported ADG heritability estimates in a population of young Charolais bulls on an 84 d performance test of 0.34, while Arthur et al. (2001b) reported heritability estimates of 0.28 for ADG in a population of Angus bulls and heifers on a 70 d test. In a mixed population of Angus, Hereford and Shorthorn cattle heritability estimates were maximized with a 70 d test ($h^2 = 0.35$) and decreased as subsequent test days were added until day 119 ($h^2 = 0.28$) (Archer, 1997). The lower heritability estimates experienced in the current analysis could be due to the increased variation among breed composition in the population, although breed effects and heterosis were fitted in all of the models. In addition, not all animals in the present study were tested for the same number of days and the number of mid-test weights collected fluctuated. Varying test lengths ranging from minimum of 62 to 148 d could have increased the amount of unexplained residual variation seen in the population.

Genetic correlations among traits within sexes were strong and positive, meaning that on average, as one trait increased the other did as well. Genetic correlations among traits between

steers and heifers were estimable through pedigree relationships. The strong correlations between on-test ADG and PWG in both steers and heifers suggests PWG is a viable substitute for on-test ADG when evaluating feed efficiency or supplement ADG data when test periods are shortened. If PWG was used as an alternative measure for on-test ADG to predict feed efficiency, it could allow for a shorter 35 d intake test as supported by previous studies (Archer et al., 1997; Wang et al., 2006).

Breed differences with standard errors are specified in Tables 2.4-2.9 with breed contrast located above the diagonal being quantified by subtracting the row breed from the column breeds. The group of breed differences among the 18 AI sired breeds was statistically significant (17 degree of freedom test) for both steers and heifers for all three traits (ADFI, ADG and PWG). Among PWG, ADG, and ADFI results, individual pairwise breed comparisons between steer and heifer ADG results were not as significant as either PWG or ADFI. Both Angus steers and heifers had the highest ADFI records when compared to the other 17 breeds involved in the analysis. Angus heifers had the largest PWG recorded for all 18 AI sire breeds. Both individual direct ($F_c < 5.26$) and maternal heterosis ($F_c < 3.99$) had significant impacts on growth and feed intake. Heterosis effects resulted in increased ADFI, ADG and PWG measures for both steers and heifers, suggesting crossbred cattle have higher both intake and gain more than the average of their purebred counterparts. These heterosis effects on ADFI echo reports in previous literature (Elzo et al., 2009; Rolfe et al., 2011) showing crossbred cattle have greater feed intake levels than purebred animals.

Conclusions

ADFI and PWG traits for both steers and heifer were moderately heritable in this study, supporting the fact that genetic selection for these traits is possible. In return, using a

combination of intake and gain data should allow for the genetic selection of feed efficiency. The correlations between steer and heifer PWG and on-test ADG were high in the current study. This suggests PWG data could be used to replace or supplement on-test ADG data to derive feed efficiency phenotypes for producer selection. If PWG was used as an alternative measure to predict feed efficiency, it could allow for a shorter 35 d intake test as supported by previous studies. A shorter test would allow more animals to be tested annually through a given set of facilities, at a lower cost per animal. Testing a greater number of animals facilitates increasing selection intensity with a resultant increase in the overall rate of genetic change of feed efficiency.

Table 2.1 Descriptive statistics for steer (S) and heifer (H) average daily feed intake (ADFI), average daily gain (ADG) and postweaning gain (PWG).

Trait	Number	Mean (kg)	Maximum	Minimum	Standard Error	Standard Deviation
SADFI	3,212	4.30	7.85	0.75	0.010	0.67
SADG	3,212	0.90	2.13	-0.27	0.005	0.26
SPWG	3,211	1.39	2.13	0.64	0.003	0.19
HADFI	2,394	3.52	5.89	0.78	0.012	0.58
HADG	2,394	0.46	1.56	-0.28	0.005	0.22
HPWG	2,392	0.88	1.50	0.14	0.004	0.21

Table 2.2 Estimates for additive genetic variance (σ_a^2) and phenotypic variance (σ_p^2) for steer (S) and heifer (H) average daily feed intake (ADFI), average daily gain (ADG), and postweaning gain (PWG).

Trait	σ_a^2	σ_p^2
SADFI	0.5820	1.3598
SADG	0.0210	0.2369
SPWG	0.0454	0.1250
HADFI	0.4167	1.0656
HADG	0.0145	0.1053
HPWG	0.0357	0.0844

Table 2.3 Heritability estimates (on diagonal SE below), genetic correlations (below diagonal SE below), and residual correlations (above diagonal SE below) for steer (S) and heifer (H) average daily feed intake (ADFI), average daily gain (ADG) and postweaning gain (PWG).

Trait	SADFI	SADG	SPWG	HADFI	HADG	HPWG
SADFI	0.43 (0.05)	0.46 (0.03)	0.70 (0.03)			
SADG	0.73 (0.12)	0.09 (0.03)	0.35 (0.03)			
SPWG	0.58 (0.06)	0.81 (0.14)	0.36 (0.05)			
HADFI	0.71 (0.09)	0.66 (0.20)	0.65 (0.09)	0.39 (0.05)	0.32 (0.04)	0.49 (0.04)
HADG	0.51 (0.15)	0.39 (0.27)	0.71 (0.15)	0.64 (0.12)	0.14 (0.04)	0.37 (0.04)
HPWG	0.47 (0.09)	0.67 (0.20)	0.91 (0.08)	0.77 (0.05)	0.65 (0.12)	0.42 (0.05)

Table 2.4 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for steer ADFI.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		363	132	440	853	349	594	82	259	662	240	558	467	567	744	535	18	549
HH ²	132		-231	77	494	-14	231	-281	-104	299	-118	195	104	204	381	172	-340	186
AR ³	127	132		308	726	218	463	-50	127	535	113	426	336	435	617	404	-109	417
SH ⁴	145	145	145		417	-91	154	-358	-181	222	-195	118	27	127	308	95	-417	109
DS ⁵	304	95	304	304		-508	-263	-776	-599	-191	-612	-295	-390	-290	-109	-318	-835	-308
BM ⁶	159	159	159	163	308		245	-268	-91	313	-104	209	118	218	395	186	-327	200
BR ⁷	159	159	159	163	313	172		-513	-336	68	-349	-36	-127	-27	154	-59	-572	-45
BN ⁸	154	154	150	163	304	163	172		177	581	163	476	386	485	667	454	-59	467
SG ⁹	150	154	150	154	308	168	168	163		404	-14	299	209	308	490	277	-236	290
BV ¹⁰	159	159	159	163	313	177	172	172	168		-422	-104	-195	-95	82	-127	-644	-113
CH ¹¹	132	136	132	150	304	159	159	154	154	159		318	222	322	503	295	-222	304
CA ¹²	150	154	150	159	308	168	168	168	159	168	154		-91	9	186	-23	-540	-9
GV ¹³	127	127	127	141	299	154	154	150	145	154	127	145		100	281	68	-445	82
LM ¹⁴	127	132	127	141	299	154	154	150	145	154	132	150	122		177	-32	-544	-18
MA ¹⁵	150	154	150	159	304	163	168	163	159	168	154	163	145	150		-209	-726	-200
SA ¹⁶	150	154	150	154	313	168	168	168	159	168	154	163	145	145	163		-517	14
SM ¹⁷	132	132	132	145	304	159	159	154	150	159	132	150	127	127	150	150		526
TA ¹⁸	308	308	308	308	381	313	318	313	313	318	313	318	308	308	313	318	308	4.23

¹Angus
²Hereford
³Red Angus
⁴Shorthorn
⁵South Devon

⁶Beefmaster
⁷Bahman
⁸Brangus
⁹Santa Gertrudis
¹⁰Braunvieh

¹¹Charolais
¹²Chiangus
¹³Gelbvieh
¹⁴Limousin
¹⁵Maine Anjou

¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-value.** (P < 0.05)
Bold differences = sign. (P < 0.01) ind.

Table 2.5 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for steer ADG.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		23	73	54	177	-41	122	-9	-68	73	-32	50	73	5	77	59	-18	136
HH ²	45		54	32	154	-64	100	-27	-91	50	-54	27	50	-14	59	36	-41	113
AR ³	41	45		-18	104	-113	50	-82	-141	-5	-104	-27	0	-68	5	-14	-91	59
SH ⁴	50	50	50		122	-95	68	-64	-122	18	-86	-5	18	-50	27	5	-73	82
DS ⁵	118	122	118	122		-218	-54	-181	-245	-104	-209	-127	-104	-172	-95	-118	-195	-41
BM ⁶	59	59	59	59	122		163	32	-27	109	9	86	113	45	118	100	23	177
BR ⁷	59	59	59	59	122	64		-132	-191	-50	-154	-73	-50	-118	-45	-64	-141	14
BN ⁸	54	54	54	59	122	64	64		-64	77	-23	54	82	14	86	68	-9	141
SG ⁹	54	54	54	54	122	59	59	59		141	36	118	141	73	150	127	50	204
BV ¹⁰	59	59	59	59	122	64	64	64	59		-104	-23	5	-64	9	-14	-86	64
CH ¹¹	50	45	45	50	118	59	59	59	54	59		82	104	36	109	91	14	168
CA ¹²	54	54	54	54	122	64	127	59	54	59	54		27	-41	32	9	-64	86
GV ¹³	45	45	41	50	118	54	54	54	50	54	45	50		-68	5	-14	-91	64
LM ¹⁴	45	45	41	50	118	54	54	54	50	54	45	50	41		73	54	-23	127
MA ¹⁵	54	54	54	54	122	59	59	59	54	59	54	59	50	50		-23	-95	54
SA ¹⁶	54	54	54	54	122	59	59	59	54	59	54	54	50	50	54		-77	77
SM ¹⁷	45	45	45	50	118	59	54	54	50	54	45	54	41	41	54	50		154
TA ¹⁸	122	122	122	122	150	122	122	122	122	122	122	122	118	118	122	122	118	1.85

¹Angus
²Hereford
³Red Angus
⁴Shorthorn
⁵South Devon

⁶Beefmaster
⁷Bahman
⁸Brangus
⁹Santa Gertrudis
¹⁰Braunvieh

¹¹Charolais
¹²Chiangus
¹³Gelbvieh
¹⁴Limousin
¹⁵Maine Anjou

¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-value.** (P < 0.05)
Bold differences = sign. (P < 0.01) ind.

Table 2.6 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for steer PWG.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		54	50	113	349	141	327	136	91	200	45	159	141	145	200	186	-14	163
HH ²	36		-5	59	295	86	272	82	36	145	-9	104	82	91	145	132	-73	109
AR ³	36	36		64	299	91	277	86	41	150	-5	109	91	95	150	136	-64	113
SH ⁴	41	45	41		236	27	213	23	-23	86	-64	50	27	32	86	73	-127	50
DS ⁵	91	91	91	91		-209	-27	-213	-259	-150	-304	-191	-213	-204	-150	-163	-367	-186
BM ⁶	45	45	45	50	91		181	-5	-50	59	-95	18	-5	5	59	45	-159	23
BR ⁷	45	45	45	50	95	50		-191	-236	-127	-277	-163	-186	-181	-127	-141	-340	-159
BN ⁸	45	45	45	50	91	50	50		-45	64	-86	27	5	9	64	50	-150	32
SG ⁹	45	45	45	45	95	50	50	50		109	-45	68	50	54	109	95	-104	73
BV ¹⁰	45	45	45	50	95	50	50	50	50		-150	-41	-59	-54	0	-14	-213	-36
CH ¹¹	41	41	41	45	91	50	45	45	45	45		113	91	95	150	141	-64	118
CA ¹²	45	45	45	45	95	50	50	50	45	50	45		-23	-18	36	27	-177	5
GV ¹³	36	36	36	41	91	45	45	45	41	45	36	45		5	59	50	-154	27
LM ¹⁴	36	36	36	41	91	45	45	45	45	45	381	45	36		54	41	-159	18
MA ¹⁵	45	45	45	45	91	50	50	50	45	50	45	50	45	45		-14	-213	-32
SA ¹⁶	45	45	45	45	95	50	50	50	45	50	45	45	41	45	45		-204	-23
SM ¹⁷	36	41	36	41	91	45	45	45	45	45	41	45	36	36	45	45		181
TA ¹⁸	91	91	91	91	113	95	95	95	95	95	95	95	91	91	95	95	91	5.86

¹Angus
²Hereford
³Red Angus
⁴Shorthorn
⁵South Devon

⁶Beefmaster
⁷Bahman
⁸Brangus
⁹Santa Gertrudis
¹⁰Braunvieh

¹¹Charolais
¹²Chiangus
¹³Gelbvieh
¹⁴Limousin
¹⁵Maine Anjou

¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-value.** (P < 0.05)
Bold differences = sign. (P < 0.01) ind.

Table 2.7 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for heifer ADFI.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		435	304	458	708	703	612	259	467	835	404	476	327	667	499	531	236	880
HH ²	122		-132	23	272	268	177	-172	36	399	-32	41	-109	231	64	95	-200	445
AR ³	118	122		154	404	399	308	-41	168	535	100	172	23	363	195	227	-68	576
SH ⁴	136	136	136		249	245	154	-200	9	376	-54	18	-132	209	41	73	-222	422
DS ⁵	290	290	295	299		-5	-95	-445	-236	132	-304	-231	-381	-41	-209	-177	-472	172
BM ⁶	154	154	154	159	299		-91	-440	-231	132	-299	-227	-376	-36	-204	-172	-467	177
BR ⁷	145	145	145	150	299	168		-349	-141	222	-209	-136	-286	54	-113	-82	-376	268
BN ⁸	145	145	145	154	295	159	159		209	576	141	213	68	404	236	268	-23	617
SG ⁹	141	141	136	145	299	159	154	154		367	-68	5	-141	195	27	59	-231	408
BV ¹⁰	141	141	136	145	299	163	154	154	145		-435	-358	-508	-172	-336	-304	-599	45
CH ¹¹	122	127	122	136	295	154	145	150	141	141		73	-77	263	95	127	-168	476
CA ¹²	136	136	132	141	295	159	150	154	145	145	136		-150	191	23	54	-240	404
GV ¹³	113	118	113	132	290	145	141	141	132	132	118	127		340	172	204	-91	553
LM ¹⁴	118	118	113	132	290	150	141	141	132	132	118	127	109		-168	-136	-431	213
MA ¹⁵	136	141	136	145	295	159	154	154	145	145	141	145	132	132		32	-263	381
SA ¹⁶	141	141	136	145	299	163	154	154	145	150	141	145	132	132	145		-295	349
SM ¹⁷	127	127	127	141	295	159	150	150	141	145	127	141	118	122	141	141		644
TA ¹⁸	259	259	259	263	331	268	268	259	268	263	259	263	254	254	259	268	263	3.89

¹Angus
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⁸Brangus
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¹¹Charolais
¹²Chiangus
¹³Gelbvieh
¹⁴Limousin
¹⁵Maine Anjou

¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-value.** (P < 0.05)
Bold differences = sign. (P < 0.01) ind

Table 2.8 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for heifer ADG.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		32	18	54	-50	68	86	82	32	145	41	77	27	68	45	86	18	177
HH ²	32		-9	23	-82	41	54	50	0	113	9	45	-5	36	14	59	-14	145
AR ³	32	32		36	-68	50	64	64	9	122	18	59	5	45	23	68	-5	154
SH ⁴	36	36	36		-104	14	32	27	-23	91	-18	23	-27	14	-9	32	-36	122
DS ⁵	91	91	91	91		118	136	132	82	195	91	127	77	118	95	136	68	227
BM ⁶	45	45	45	45	91		14	9	-41	73	-32	5	-45	-5	-27	18	-54	104
BR ⁷	41	41	41	41	91	50		-5	-54	59	-45	-9	-59	-18	-41	0	-68	91
BN ⁸	41	41	41	45	91	45	45		-50	64	-41	-5	-54	-14	-36	5	-64	95
SG ⁹	41	41	36	41	91	45	41	45		113	9	45	-5	36	14	54	-14	145
BV ¹⁰	41	41	36	41	91	45	41	45	41		-104	-68	-118	-77	-100	-59	-127	32
CH ¹¹	36	36	32	36	91	45	41	41	36	41		36	-14	27	5	50	-23	136
CA ¹²	36	36	36	41	91	45	41	45	41	41	36		-50	-9	-32	9	-59	100
GV ¹³	32	32	32	36	91	41	41	41	36	36	32	36		41	18	59	-9	150
LM ¹⁴	32	32	32	36	91	41	41	41	36	36	32	36	32		-23	23	-50	109
MA ¹⁵	36	41	36	41	91	45	41	45	41	41	41	41	36	36		45	-27	132
SA ¹⁶	36	41	36	41	91	45	41	45	41	41	36	41	36	36	41		-73	86
SM ¹⁷	36	36	36	41	91	45	41	45	41	41	36	36	32	32	41	41		159
TA ¹⁸	77	77	77	77	100	82	82	77	77	77	77	77	77	77	77	77	77	1.65

¹Angus
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¹¹Charolais
¹²Chiangus
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¹⁴Limousin
¹⁵Maine Anjou

¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-values** (P < 0.05)
Bold differences = sign. (P < 0.01) ind

Table 2.9 Breed differences (g, above diagonal, Rows - Columns) and individual SE (g, below diagonal) for heifer PWG.

	AN ¹	HH ²	AR ³	SH ⁴	DS ⁵	BM ⁶	BR ⁷	BN ⁸	SG ⁹	BV ¹⁰	CH ¹¹	CA ¹²	GV ¹³	LM ¹⁴	MA ¹⁵	SA ¹⁶	SM ¹⁷	TA ¹⁸
AN ¹		54	68	109	9	141	231	136	127	277	86	122	109	159	100	150	68	263
HH ²	36		14	54	-45	91	177	82	73	222	32	68	54	104	45	95	18	209
AR ³	32	36		41	-59	73	163	68	59	209	18	54	41	91	32	82	0	195
SH ⁴	41	41	41		-100	32	122	27	18	168	-23	14	0	50	-9	41	-41	154
DS ⁵	82	82	82	86		132	222	127	118	268	77	113	100	150	91	141	59	254
BM ⁶	45	45	45	45	86		86	-9	-18	136	-59	-18	-32	18	-41	5	-73	122
BR ⁷	41	41	41	41	86	45		-95	-104	45	-145	-109	-122	-73	-132	-82	-159	32
BN ⁸	41	41	41	45	82	45	45		-9	141	-50	-14	-27	23	-36	14	-64	127
SG ⁹	41	41	41	41	86	45	45	45		150	-41	-5	-18	32	-27	23	-54	136
BV ¹⁰	41	41	41	41	86	45	45	45	41		-191	-154	-168	-118	-177	-127	-209	-14
CH ¹¹	36	36	36	41	86	45	41	41	41	41		36	27	77	14	64	-14	177
CA ¹²	36	41	36	41	86	45	41	45	41	41	41		-14	36	-23	27	-54	141
GV ¹³	32	32	32	36	82	41	41	41	36	36	32	36		50	-9	36	-41	154
LM ¹⁴	32	32	32	36	82	41	41	41	36	36	32	36	32		-59	-14	-91	104
MA ¹⁵	41	41	41	41	82	45	45	45	41	41	41	41	36	36		50	-32	163
SA ¹⁶	41	41	41	41	86	45	45	45	41	41	41	41	36	36	41		-77	113
SM ¹⁷	36	36	36	41	86	45	41	41	41	41	36	41	32	36	41	41		195
TA ¹⁸	73	73	73	77	95	77	77	73	77	77	73	77	73	73	73	77	73	4.87

¹Angus
²Hereford
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⁶Beefmaster
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⁸Brangus
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¹¹Charolais
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¹⁶Salers
¹⁷Simmental
¹⁸Tarentaise
***F-value.** (P < 0.05)
Bold differences = sign. (P < 0.01) ind

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Chapter 3 - Indices to Improve Feed Efficiency

Introduction

Evaluating feed efficiency of beef cattle has evolved from relying on single trait selection for increased gain to extensive use of multiple trait selection combining measures of gain and feed intake. Phenotypes such as residual feed intake or residual gain place greater emphasis on one component trait at a time to select for feed efficiency. Studies have suggested using a selection index for feed efficiency is more efficient than directly selecting on one component trait or selecting on a ratio of component traits (Hazel and Lush, 1943; Lin 1980; Gunsett, 1984). A 70 d gain and intake test is recommended by the Beef Improvement Federation (BIF) Guidelines (2010) to accurately test for feed efficiency. Previous literature has suggested that a shortened test period of 35 d could be used to accurately assess feed intake in growing beef cattle, but not average daily gain (ADG). (Archer et al., 1997; Wang et al., 2006). Strong genetic correlation estimates for growing steers (0.81) and heifers (0.65) between on-test ADG, as derived through regression, and postweaning gain as calculated by National Cattle Evaluation (PWG) suggest PWG is a reliable proxy for ADG. Postweaning gain is the difference between 365-d and 205-d age adjusted weights. This PWG value could be used in an index with shorter intake tests (35 d) to select animals for improved feed efficiency. Under this paradigm, producers could decrease costs per animal and increase genetic change by testing a greater number of animals per year. Objectives of this study were to compare two alternative indices for feed efficiency, and to quantify the genetic response to selection for feed efficiency combining an intake test with PWG data.

Materials & Methods

Data on 5,606 growing steers and heifers for on-test average daily gain (ADG), on-test average daily feed intake (ADFI), and postweaning gain (PWG) were obtained from the U.S. Meat Animal Research Center in Clay Center, NE. Animal procedures were approved by IACUC at USMARC in accordance with FASS (2010) guidelines. Genetic (co)variances and EBV were estimated using a six trait animal mixed model with ADG, ADFI, and PWG as dependent variables for both steers and heifers. Indices combining EBVs for ADFI and ADG and for ADFI and PWG were evaluated. For each index, the weighting of gain was arbitrarily set to 1.0 and the weighting for ADFI was the negative of the average of the intra-contemporary group ratio of mean PWG or ADG divided by mean ADFI, as described by Lin (1980). Means of ADG, ADFI, and PWG of the 41 steer and 39 heifer feed efficiency contemporary groups are shown in Table 3.1. Values were combined with EBV to compute two aggregate genotypes values per animal ($H_{ADFI, ADG}$; $H_{ADFI, PWG}$).

The relationship between the two indices for both steers and heifers were analyzed using the CORR procedures of SAS (SAS Inst. Inc., Cary, NC). Both Pearson and Spearman Rank correlations were estimated using this procedure in SAS to identify the strength of the linear relationship between $H_{ADFI, ADG}$ and $H_{ADFI, PWG}$.

The number of animals tested per year and relative testing costs of the on-test ADG and ADFI index was calculated based on a 91 d test (21 d warm-up period and 70 d intake test). A 56 d test standard (21 d warm-up period plus 35 d shortened intake test) was used to predict the number of animals tested and relative costs using PWG data with ADFI. Table 3.2 and 3.3 includes the genetic and phenotypic (co)variances used to derive the genetic selection index values and heritability estimates of efficiency for the 56 and 91 d tests. Heritability estimates were determined by the following equation:

$$h^2 = (\mathbf{b}'\mathbf{G}\mathbf{v})/(\mathbf{v}'\mathbf{C}\mathbf{v})$$

where $\mathbf{b}'\mathbf{G}\mathbf{v}$ is the covariance of the index and $\mathbf{v}'\mathbf{C}\mathbf{v}$ is the variance of the aggregate genotype.

Response per generation was predicted by the following:

$$\Delta\mathbf{BV}/\text{generation} = \mathbf{r}_{\mathbf{b}\mathbf{v},\mathbf{b}\mathbf{v}}\mathbf{i}\sigma_{\mathbf{a}}$$

where $\mathbf{r}_{\mathbf{b}\mathbf{v},\mathbf{b}\mathbf{v}}$ is the accuracy of the index (the square root of heritability), \mathbf{i} is overall selection intensity, and $\sigma_{\mathbf{a}}$ is the genetic variation of the aggregate genotype.

Results & Discussion

Descriptive statistics for EBVs and index values are located in Table 3.4. More negative ADFI EBV indicates an animal with a more desirable feed intake value. A more positive ADG or PWG indicates an animal with a more desirable gain. Therefore, a greater aggregate genotype value represents an animal with more desirable feed efficiency. A more negative value represents a less efficient animal.

Indices used to combine weighting factors and EBV are as follows:

steer,

$$\mathbf{H}_{\text{ADG, ADFI}} = \text{ADGEBV} + (-0.2030) \text{ADFIEBV}$$

$$\mathbf{H}_{\text{PWG, ADFI}} = \text{PWGEBV} + (-0.3150) \text{ADFIEBV};$$

heifer,

$$\mathbf{H}_{\text{ADG, ADFI}} = \text{ADGEBV} + (-0.1273) \text{ADFIEBV}$$

$$\mathbf{H}_{\text{PWG, ADFI}} = \text{PWGEBV} + (-0.2493) \text{ADFIEBV}.$$

Results from the correlation analysis differ between steers and heifers. Examining the steer Pearson and Spearman correlations (0.96 and 0.96, $P < 0.0001$), there appears to be very little loss in accuracy when using the index involving PWG rather than ADG to quantify feed efficiency due to the strength of the relationship between $\mathbf{H}_{\text{ADG, ADFI}}$ and $\mathbf{H}_{\text{PWG, ADFI}}$. Therefore,

using PWG data to calculate an index of efficiency is acceptable. Although strong correlations were seen in the steer populations, the same relationship between $H_{ADG, ADFI}$ and $H_{PWG, ADFI}$ did not occur in the female population. Both the heifer Pearson and Spearman correlations (0.45 and 0.43, $P < 0.0001$) resulted in only moderate correlations, indicating a large amount of unexplained variation fluctuated between the two indices or a lack of a linear relationship between the two genotypes.

The heritability of efficiency and differences in relative annual progress using the two separate indices for both steers and heifers can be seen in Table 3.5 and 3.6. Both steers and heifers realized a predicted 62% increase in the relative animals tested per year when the index employing a shortened 35 d intake test with PWG data was used. Increasing the number of animals tested caused the relative cost per tested animal to decrease 38%. Greater heritability estimates of efficiency were predicted with the 56 d index, likely due to higher PWG heritability estimates predicted when analyzing gain traits separately. Both steers and heifers were predicted to have greater change per generation in feed efficiency, 24% and 9% respectively, when the 56 d index with PWG was used versus the genetic change realized from testing animals for feed efficiency with the longer test using ADG. Much of this increase is due to the increased selection intensity realized when a shortened 35 d intake test is used allowing for more animals to be tested per year.

Conclusions

These findings support using PWG data in combination with ADFI to determine efficient steers, lessen costs, and increase feed efficiency genetic change per year. In doing this, quantifying feed efficiency can be done in a more cost effective manner by collecting feed intake data on a larger number of selection candidates. The corresponding increase in selection intensity

could result greater overall genetic change per year. Heifer correlation estimates between the two indices were lower in this study. However, greater heritability estimates reported for the 56 d test, as well as the increased selection intensity resulting from a shorter test, could support using a 35 d intake test with PWG data to quantify feed efficiency in developing females as well.

Table 3.1 Contemporary group means for steer (S) and heifer (H) average daily feed intake (ADFI) (kg), postweaning gain (PWG) (kg), and average daily gain (ADG) (kg).

	Sex	N	ADFI	PWG	ADG		Sex	N	ADFI	PWG	ADG
1	S	123	8.12	3.01	2.00	41	H	10	8.09	1.88	1.26
2	S	138	8.36	3.07	1.96	42	S	7	10.55	3.03	1.89
3	S	261	8.92	3.16	1.91	43	H	29	7.76	1.84	1.18
4	H	117	8.29	2.20	1.20	44	S	34	9.89	2.94	1.70
5	H	122	9.09	1.85	1.28	45	H	54	8.00	2.28	0.76
6	S	259	8.75	3.03	2.04	46	S	20	10.50	3.19	2.18
7	H	119	7.70	2.12	0.91	47	H	61	7.87	2.22	0.75
8	H	110	7.93	1.80	1.04	48	S	54	10.31	3.11	2.14
9	S	257	8.57	2.99	1.74	49	H	83	7.79	2.18	0.75
10	H	113	7.45	1.95	1.29	50	S	100	9.78	2.96	1.79
11	H	101	8.20	1.84	1.62	51	H	35	7.82	2.24	0.69
12	S	213	7.98	2.78	1.85	52	S	32	10.47	3.14	2.04
13	H	51	6.81	0.95	0.15	53	H	66	7.65	2.19	1.61
14	S	34	8.57	2.79	1.85	54	S	68	9.54	3.44	2.26
15	H	74	6.45	0.95	0.22	55	H	53	7.59	2.28	1.62
16	S	91	8.51	2.76	1.85	56	S	71	9.89	3.39	2.35
17	S	10	6.40	1.08	0.16	57	H	44	7.40	2.00	1.25
18	H	46	6.24	1.11	0.66	58	S	33	10.13	3.05	2.09
19	H	16	10.57	2.90	2.11	59	H	75	7.60	2.09	1.36
20	H	119	6.70	1.24	0.68	60	S	128	11.03	3.27	2.19
21	S	104	10.37	2.84	1.91	61	H	48	8.20	2.15	1.38
22	S	40	6.82	1.26	0.61	62	S	30	10.22	3.07	1.97
23	S	16	9.97	2.81	1.78	63	H	51	8.35	8.35	8.35
24	H	57	6.86	1.85	0.57	64	S	54	9.67	3.46	2.07
25	S	74	9.86	3.10	1.65	65	H	38	8.18	2.32	1.38
26	H	18	7.10	2.04	0.67	66	S	34	9.62	3.39	2.13
27	S	22	10.29	3.23	1.74	67	H	21	7.53	2.17	1.41
28	H	56	7.18	1.95	0.70	68	S	30	9.02	3.30	2.07

29	S	44	9.79	3.17	1.66	69	H	38	7.46	2.20	1.30
30	H	67	7.38	1.84	0.87	70	S	62	10.10	3.18	1.84
31	S	74	10.18	3.20	3.00	71	H	70	8.15	2.31	1.39
32	H	103	7.25	1.66	0.75	72	S	75	10.74	3.27	1.92
33	S	92	9.96	2.99	2.92	73	H	35	7.78	2.40	1.43
34	S	64	10.47	2.50	1.79	74	S	55	10.13	3.18	1.74
35	S	61	10.45	2.64	1.69	75	H	42	9.22	2.19	0.82
36	S	62	10.30	2.55	1.65	76	S	48	10.24	3.23	1.76
37	H	54	7.74	1.94	0.79	77	H	33	9.64	2.18	0.81
38	S	92	9.69	3.20	2.66	78	S	40	10.72	3.25	1.75
39	H	74	8.09	2.05	1.25	79	H	57	9.13	2.28	0.84
40	S	82	10.33	3.11	1.80	80	S	58	10.06	3.44	1.80

Table 3.2 Phenotypic (co)variance for steer (S) and heifer (H) average daily feed intake (ADFI), average daily gain (ADG), and postweaning gain (PWG).

Trait	SADFI	SADG	SPWG	HADFI	HADG	HPWG
SADFI	1.360 (0.37)					
SADG	0.270 (0.01)	0.237 (0.60)				
SPWG	0.271 (0.01)	0.072 (0.003)	0.125 (0.33)			
HADFI				1.070 (0.33)		
HADG				0.128 (0.76)	0.105 (0.31)	
HPWG				0.181 (0.77)	0.040 (0.002)	0.084 (0.26)

Table 3.3 Phenotypic (co)variance for steer (S) and heifer (H) average daily feed intake (ADFI), average daily gain (ADG), and postweaning gain (PWG).

Trait	SADFI	SADG	SPWG	HADFI	HADG	HPWG
SADFI	0.582 (0.08)					
SADG	0.080 (0.02)	0.021 (0.01)				
SPWG	0.095 (0.02)	0.025 (0.01)	0.045 (0.01)			
HADFI				0.417 (0.06)		
HADG				0.050 (0.01)	0.015 (0.004)	
HPWG				0.093 (0.01)	0.015 (0.004)	0.036 (0.004)

Table 3.4 Descriptive statistics for steer and heifer average daily feed intake EBV (ADFIEBV, average daily gain EBV (ADGEBV), and postweaning gain EBV (PWGEBV) and steer and heifer average daily gain and average daily feed intake index ($H_{ADG, ADFI}$) and steer and heifer postweaning gain and average daily feed intake index ($H_{PWG, ADFI}$).

Variable	Mean	Std. error	Maximum	Minimum
Heifer ADGEBV	0.0009	0.0646	0.2348	-0.2561
Heifer ADFIEBV	0.0032	0.4053	1.8764	-2.0113
Heifer PWGEBV	-0.0003	0.1261	0.4909	-0.4664
Heifer $H_{ADG, ADFI}$	0.0004	0.0357	0.1837	-0.1316
Heifer $H_{PWG, ADFI}$	0.0002	0.0698	0.3078	-0.3458
Steer ADGEBV	0.0007	0.0837	0.3295	-0.3602
Steer ADFIEBV	0.0139	0.4850	3.1960	-3.4710
Steer PWGEBV	0.0005	0.1418	0.5673	-0.5851
Steer $H_{ADG, ADFI}$	-0.0026	0.0645	0.4849	-0.3631
Steer $H_{PWG, ADFI}$	-0.0050	0.1450	1.0608	-0.8554

Table 3.5 Relative efficiency of 56 d and 91 d tests for steers.

	91 d Test ^a	56 d Test ^b
Heritability of gain trait	0.09	0.36
Genetic correlation (Gain, Feed Intake)	0.73	0.58
Relative number tested/year	1.00	1.62
Heritability of efficiency	0.15	0.48
Relative cost/tested animal	100%	62%
Selection Intensity (N = 5)	5% i = 2.06	3% i = 2.27
Genetic Change in index per generation	9%	33%

^a91 d Test included a 21 d warm up period with a 70 d gain and intake test.

^b56 d test included a 21 d warm up period with a 35 d intake test using post weaning gain data.

Table 3.6 Relative efficiency of 56 d and 91 d tests for heifers.

	91 d Test ^a	56 d Test ^b
Heritability of gain trait	0.14	0.42
Genetic correlation (Gain, Feed Intake)	0.64	0.77
Relative number tested/year	1.00	1.62
Heritability of efficiency	0.10	0.27
Relative cost/tested animal	100%	62%
Selection Intensity (N = 5)	5% i = 2.06	3% i = 2.27
Genetic Change in index per generation	6%	15%

^a91 d Test included a 21 d warm up period with a 70 d gain and intake test.

^b56 d test included a 21 d warm up period with a 35 d intake test using postweaning gain data.

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