WINSLOW, BENJAMIN LEWIS. Relationships among Feed Utilization and Performance Traits in Developing Angus Heifers. (Under the direction of Gary R. Hansen and Joseph P. Cassady.)

The objective was to investigate relationships among feed utilization traits, other economically important traits, and potential indicators of feed utilization efficiency. Data were from 4 groups (years) of Angus heifers (n = 208) at the Upper Piedmont Research Station, Reidsville, NC. Dry matter intake (DMI) was recorded during an 84-d trial. Heifers were fed a roughage-based ration formulated for 0.91 kg/d gain. Heifers were weighed at the beginning, end, and every 14 d during the trial. Means for on-test age and weight were 273 ± 1.9 d and 263 ± 2.5 kg. At the beginning, middle, and end of the trial, hip height (HipHt) was recorded, blood was collected for thyroid hormone assays, and heifers were ultrasonically scanned for fat content and ribeye area. Chute exit velocity (EV) and temperament score (TS) were recorded. In Year 4, heifers were scored for reproductive tract maturity. Means for DMI and ADG were 6.6 ± 0.08 kg/d and 0.85 ± 0.015 kg/d, respectively. Feed conversion ratio (FCR) was defined as DMI/ADG, and had a mean of 8.3 ± 0.17. Partial efficiency of growth (PEG) was defined as ADG / (portion of DMI for growth) and had a mean of 0.35 ± 0.015. Residual feed intake was calculated by three methods. For RFIsca, intake was predicted with an equation using mid-test body weight (MidWt). Intake for RFInrc was predicted with equations for amounts of feed required for maintenance and growth, based on mid-test metabolic weight (MetMW) and ADG. For RFlreg, predicted intake was modeled by phenotypic regression of DMI on covariates MetMW and ADG. Means for RFIsca, RFInrc, and RFlreg were -1.95 ± 0.17, -1.13 ± 0.116, and 0 ± 0.031 kg/d, respectively. Partial phenotypic correlations (adjusted for year) among efficiency traits (FCR, PEG, RFIsca,
RFInrc, RFIreg) were statistically significant (P < 0.01) (negative for PEG, positive among others). Efficiency traits were also phenotypically correlated with DMI (P < 0.01) (negative for PEG). A strong, negative phenotypic correlation (-0.67; P < 0.01) between FCR and ADG was observed, while RFIreg was, by design, phenotypically independent of ADG. Feed conversion ratio was also phenotypically correlated with MidWt (0.32; P < 0.01) and HipHt (0.15; P < 0.05). An efficiency trait’s phenotypic relationships with ultrasound traits generally reflected its relationship with size. Measures of thyroid hormone T3 were phenotypically correlated negatively with DMI and positively with ADG, and thus were significantly correlated with all efficiency traits except RFIreg. Feed conversion ratio was phenotypically correlated with TS but not EV, while RFIreg was independent of both. Spearman rank correlations among efficiency traits were lowest for RFIreg. From genetic analysis (MTDFREML; Animal model; 5-generation pedigree; Year as fixed effect), the positive genetic correlation (0.41 ± 0.313) between RFIreg and ADG was unfavorable, though not statistically different from zero. Among heifers grouped by RFI breeding value, significant differences were observed for DMI, FCR, and reproductive tract score. It was concluded that, among efficiency traits evaluated, RFIreg was least correlated with production traits.
Relationships Among Feed Utilization and Performance Traits in Developing Angus Heifers

by
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CHAPTER 1

Literature Review
**Introduction**

In the quest to enhance profitability, beef cattle breeders historically have tended to focus more on increasing output production (e.g., maximizing weight gain or carcass merit) than on reducing input costs (Arthur et al., 2001a; Herd et al., 2003). However, escalation of feed, fuel, and fertilizer prices has helped shift attention to cost reduction and efficiency improvement. Also, technological advances have enabled individual feed intake data to be collected much more conveniently and less expensively, making integration of intake data into breeding programs more feasible. With feed costs representing the largest single expense in most beef production operations (Arthur et al., 2001a), improving feed utilization efficiency is clearly essential to lowering the overall cost of beef production. Breeders aiming to improve feed efficiency need to understand the various traits used to measure efficiency and relationships of these traits with other traits of economic significance.

**Measures of Feed Utilization Efficiency**

Because of the general correlation between feed intake and production, a look at either type of trait without consideration of the other typically yields very little, if any, information about the efficiency of production (Archer et al., 1999; Arthur et al., 2004). There is a multitude of ways in which “feed efficiency” has been measured. However, as emphasized by Archer et al. (1999), none of these indices of feed intake and production is adequately representative of total production system efficiency, which encompasses not only feed intake (for both breeding and slaughter animals) and growth, but also fertility, longevity,
and numerous other traits. Nonetheless, each method of estimating feed efficiency is somewhat useful and can contribute toward efficiency improvement when implemented correctly.

*Gross efficiency and Feed Conversion Ratio*

Gross efficiency—or often its inverse, feed conversion ratio (FCR)—is the index of feed efficiency most widely reported in the literature and is defined as the ratio of production outputs to feed inputs (Archer et al., 1999). For beef production, the output is often measured as weight change in growing cattle. Refining the production output to include only lean tissue gain is another option (Archer et al., 1999). Although gross efficiency is typically measured over a specific period of time, there are other bases for measurement that can help to eliminate the effects of scale or maturity pattern. Such alternatives include computing gross efficiency over a specified change in weight (i.e., from weight \( a \) to weight \( b \)) or on a maturity-constant basis (i.e., weight gain and feed measured as the animal matures from maturity stages \( a \) to \( b \)) (Archer et al., 1999). These procedures could reduce variation due to composition of gain and(or) to maintenance requirement differences (due to size variation), a major limitation of gross efficiency that had been recognized by Koch et al. (1963).

Gunsett (1984) identified potential problems associated with selection on a ratio-based trait, such as gross efficiency or FCR. Direct selection on a trait defined as a ratio was shown to produce a less predictable response and to be less efficient than selection on a linear index with properly weighted components (Gunsett, 1984). Before selecting on FCR, one should also consider the widely recognized, powerful correlations between gross efficiency
and many basic measures of production by livestock. For instance, with beef cattle, a review by Brelin and Brannang (1982) reported genetic correlations of -0.61 to -0.95 between growth rate and FCR. The general explanation for the relationship between this efficiency measure and production (growth rate, milk production, etc.) is that a higher proportion of the nutrients are being used for production—versus maintenance—at higher levels of production. The genetic correlations between gross efficiency and production traits are so strong, in fact, that Mrode et al. (1990), working with Hereford cattle, achieved a correlated response in FCR (-0.17 ± 0.07 kg feed/kg lean gain·year) in a line selected for lean growth rate which was greater than the direct response to selection (-0.14 ± 0.07 kg feed/kg lean gain·year) in the line selected on lean FCR. Results such as these provide strong support for the concept of improving gross efficiency without actually having to measure feed intake. However, as mentioned by Archer et al. (1999), cattle breeders aiming to improve overall efficiency through advancement (via either direct or indirect selection) in gross efficiency should be mindful of the likely correlated increase in mature size. The elevated costs associated with maintaining larger animals in the breeding herd at least partially offset the benefits of improving gross efficiency. For this reason, Archer et al. (1999) suggest that—while greater gross efficiency is virtually always beneficial in growing-only settings such as feedlots—its contribution toward industry-wide efficiency is unclear.

Maintenance efficiency

Maintenance requirement refers to that amount of feed energy required for zero change in either body weight (BW) or body energy (Ferrell and Jenkins, 1985). This energy
requirement for maintenance is often reported as kilocalories (kcal) required per kg metabolic body weight (MBW; BW^{0.75}). Archer et al. (1999) defined maintenance efficiency as the ratio of BW to feed intake at BW stasis. Accurate evaluation of maintenance requirements necessitates that the cattle be mature so that BW can be held constant (Archer et al., 1999). This stipulation translates into a large investment of time and other resources prior to determining an animal’s requirement. Fasting heat production (FHP) has been proposed as an alternative method of gauging maintenance requirement; however, there is not complete agreement as to the utility of FHP in that role (Koong et al., 1982; Shuey et al., 1993). Both maintenance efficiency and production efficiency will be discussed in more detail as components of efficiency in the mature cow herd.

*Production efficiency (Cow/calf efficiency)*

Production efficiency (PE), sometimes termed cow/calf efficiency, typically involves measuring the feed intake of a cow and her progeny during one production cycle. This period is often defined as the 12 months from the weaning of the previous calf until weaning of the present calf, although some studies have also considered post-weaning feed consumption by the calf. Production efficiency is generally expressed as weight of calf produced per unit of feed or energy intake (or as the reciprocal of this ratio). Archer et al. (1999) reported that cow/calf efficiency—while far from a perfect indicator trait—is quite likely correlated with true overall efficiency.
Partial efficiency of growth

The partial efficiency of growth (PEG) is the ratio of weight gain to feed intake—following the deduction of expected requirements for maintenance (Archer et al., 1999; Nkrumah et al., 2004). Maintenance requirement is often estimated either from table values (e.g., from NRC, 2000) and average body weight during the trial, or from a metabolic study considering energy balance of the animal (Archer et al., 1999). However, Archer et al. (1999) identified problems associated with each route. Standard values from feeding tables inherently imply no variation in the efficiency of feed use for maintenance (at a given BW). But, metabolic studies are generally not practical for large numbers of animals.

Residual feed intake

The concept of residual feed intake (RFI) was apparently first formally introduced by Koch et al. (1963). In that seminal paper, Koch and co-workers proposed adjusting feed consumption for differences in gain and in average BW maintained. The deviation between the observed consumption and that expected based upon the animal’s gain and mid-test MBW (MetMW) indicates efficiency of feed use, and has come to be known as RFI. In addition to BW and gain, other production traits of interest and any other factors affecting energy demand can be included in the intake adjustment. Residual feed intake thus allows one to identify animals that consume less feed than expected, after certain factors influencing requirements or consumption have been included in the intake prediction equation. An additional benefit of RFI over traits like FCR is that RFI—largely through its consideration of maintenance requirements due to weight—may be less affected by pre-trial environment
(Hennessy and Arthur, 2004; Nkrumah et al., 2004; Lancaster et al., 2009a).

When feed intake is predicted by phenotypic regression of intake on BW and production—as is often the case—RFI is not phenotypically correlated with those traits used to predict intake. This could lead to the belief that selection on RFI would have no effect on BW or the other production traits [e.g., average daily gain (ADG)] used in the regression. However, as demonstrated by Kennedy et al. (1993), RFI—determined through phenotypic regression—is not necessarily genetically independent of production. Working with heritabilities of 0.1, 0.3, or 0.5 for feed intake and production, and genetic and environmental correlations between these traits of 0.1, 0.5, or 0.9, they found the genetic correlation between RFI and production to range from -0.90 to 0.87. The genetic correlation between RFI and production was most favorable when feed intake and production had a weak genetic correlation (generally unlikely), but a high environmental correlation. Calculating RFI as actual intake minus expected intake predicted by genotypic regression of intake on production would allow selection on RFI to be genetically independent of production (Kennedy et al., 1993). Selecting on the basis of genotypic RFI would effectively be selection on an index for feed intake, BW, and production, that has been restricted to hold BW and production genetically constant (Kennedy et al., 1993). Determining RFI by genotypic regression requires more complete knowledge of genetic and phenotypic parameters of the component traits, but may be necessary to control correlated responses.

Another point made by Kennedy et al. (1993) is that RFI provides little or no new genetic information beyond that provided by intake and production. This was also explained by van der Werf (2004). Genetic evaluations and selection indices containing only the
constituent traits (intake, production) should be at least as accurate and effective as those including RFI. However, RFI may still have a role as an indicator of biological efficiency, especially when composition of body and growth is considered and all measurements are accurate (van der Werf, 2004).

Summary

There are several traits that may be used to gauge feed utilization efficiency. Each is accompanied by its own unique difficulties and benefits. They vary in their ease of measurement (though all require at least individual intake data) and time of measurement (growing or adult). Whichever trait is chosen as a breeder’s vehicle for improving efficiency, the breeder should attempt to minimize any undesirable correlated responses to selection.
Efficiency in the Mature Cow Herd

Maintenance efficiency

Ferrell and Jenkins (1984) estimated that around 50% of the total (feed) energy consumed in beef production is used for maintenance of the cow herd. This conclusion was derived from the observations that between 65% and 75% of the energy for beef production is used by the cows (Gregory, 1972; Klosterman and Parker, 1976), and that roughly 70% of that energy is used for maintenance requirements of the cows. Dickerson (1978) reported that about 60% of the total life cycle energy intake per unit of edible beef protein is allocated to the breeding female. Understanding variation in maintenance requirements of the cow is a key step toward improving the overall efficiency of feed utilization in beef production.

Mature size, breed, sex, environment, and physiological state are some of the factors that influence maintenance requirements (NRC, 2000). Cattle that differ in size or milk production potential, as a result of successful selection for those traits, likely have different nutrient requirements and, also, different priorities in deposition and retrieval of body tissues (Solis et al., 1988).

Solis et al. (1988) examined maintenance requirements and energetic efficiency, using dry, non-pregnant, mature cows of three beef breeds (Angus, Hereford, Brahman) and two dairy breeds (Holstein, Jersey), and their crosses. Energy required for no change in BW was determined by the regression of daily weight change (g/kg^{0.75}) against metabolizable energy (ME) intake (kcal/kg^{0.75}). There were differences among breeds for ME (kcal/kg^{0.75}) required for body weight maintenance. Angus and Brahman had lower (P < 0.05) requirements than Holstein and Jersey, while Hereford and Holstein requirements were lower.
(P < 0.05) than Jersey. Additionally, Solis et al. (1988) estimated ME requirements for energy equilibrium and also energetic efficiency (retained energy (RE) / ME intake), by regression of daily RE on ME intake. Similar to requirements for BW maintenance, they found beef breeds to have significantly lower requirements for energy equilibrium and significantly greater energetic efficiency values.

The idea that breed types capable of higher milk production require more energy for maintenance than do types with less milk production potential has been supported by many additional studies (e.g., Garrett, 1971; Thompson et al., 1983; Tyrell et al., 1974). The work of McDonald and Nielsen (2006) showed that the concept also applies to mice. Montaño-Bermudez et al. (1990) investigated the BW maintenance requirements of cows of breeds similar in size but differing in milk production (Low (L) = Hereford X Angus; Medium (M) = Red Poll X Angus; High (H) = Milking Shorthorn X Angus). Adjusting for milk production (measured by the weigh-suckle-weigh technique (Clutter and Nielsen, 1987), body condition, and BW change, they found the L group to have significantly lower ME requirements for maintenance (Montaño-Bermudez et al., 1990). Variation in milk production explained 23% of the variation in maintenance requirements (Montaño-Bermudez et al., 1990). Additionally, after accounting for weight gain and its composition, Montaño-Bermudez et al. (1990) found lower maintenance requirements for L-group calves (versus M- and H-group calves) in a post-weaning, feedlot setting. Blaxter and Wainman (1966) observed greater fasting heat production in Ayrshire steers than in Angus steers. In dry, open, mature cows, Ferrell and Jenkins (1984) found that types characterized as having high milk production potential (Jersey and Simmental, crossed with Angus or Hereford) tended to have
higher energy requirements for maintenance of BW or energy than types of lower milk production potential (Angus X Hereford crosses, and Charolais crossed with Angus or Hereford). Additionally, Ferrell and Jenkins (1984) observed that maintenance requirements, when scaled for metabolic body size (i.e., kcal/MBW), did not differ between types which differed in size but were similar in milking potential.

Solis et al. (1988) identified differing body tissue priorities—including, for example, varying fat deposition patterns—as a potential partial explanation for the differences in requirements for dairy versus beef types. Regarding fat depot preferences, Kempster’s review (1981) presented the conclusion that dairy breeds deposit a greater proportion of total fat internally and a smaller proportion subcutaneously than do British beef breeds. In agreement with this were the differences in fat deposition of L- versus M- and H-group steers reported by Montaño-Bermudez et al. (1990). Thompson et al. (1983) found that winter maintenance energy requirements (per MBW) tended to be lower for fatter Angus X Hereford cows and yet higher for fatter Angus-Holstein cows. Possible explanations for this finding include that the dairy-cross cows deposited relatively more fat internally versus subcutaneously and thus created less insulation, and also that internal adipose tissue has greater metabolic activity than peripheral depots and hence would require more energy for maintenance (Thompson et al., 1983). The findings of Smith and Baldwin (1974) and Ferrell et al. (1976) that Holstein and Jersey first-calf cows had much larger internal organs than did first-calf Herefords suggest another factor contributing to the differences in energy needs for maintenance. Similarly, Jenkins et al. (1981) reported a higher percentage of viscera from Jersey-cross than from Angus X Hereford bulls.
**Production efficiency**

Shuey et al. (1993) investigated the relationship between maintenance energy requirement (MEm) and production efficiency (PE) of Hereford X Angus first-calf heifers. A secondary objective of that study was to determine whether variation in maintenance requirements was due mainly to inherent metabolic rate (fasting heat production/MBW; FHP) or the partial efficiency of ME use for maintenance (Km; = FHP/MEm). Here, PE was defined as the weight of calf weaned, divided by the total ME consumed by the dam and as creep feed consumed by the calf, during a 12-month period in drylot. Additionally, intake of ME was adjusted for maternal BW gain. This was done to reduce bias due to the inability to meet requirements exactly, and NRC (1984) enabled the authors to estimate energy requirements for observed maternal BW gain. These first-calf dams entered the calorimeter following the weaning of their calves.

Variation in MEm has to be attributable to FHP and Km, owing to the fact that it is a function of those two variables alone. FHP and Km explained 72.5 and 27.5% of the variation in MEm, respectively (Shuey et al., 1993). This finding appeared contrary to the results obtained by Taylor et al. (1986). The conclusions of Shuey et al. (1993) did generally agree with Rompala et al. (1991), who found FHP mostly responsible for observed MEm trends in Targhee rams.

Shuey et al. (1993) found calf growth traits to account for much more of the variation in PE than did traits of the dams themselves. For Shuey et al. (1993) neither FHP nor MEm was significant (P = 0.16), and they explained very little PE variation ($R^2 = 0.04$). Partial efficiency for maintenance (Km) was not related to PE (P > 0.95). Shuey et al. (1993)
proposed that the nutrition level provided (which supported an average maternal BW gain of 0.24kg/d) could possibly have contributed to the weakness of the relationship between PE and the energy traits. Citing the suggestion by Ferrell and Jenkins (1985) that energy restriction would place higher-producing breed types at a disadvantage, Shuey et al. (1993) pointed out that their findings would support the tacit corollary that no advantage is gained by breed types (or, in their case, individuals within a breed type) with lower MEm when in an environment that is not nutritionally limiting. Shuey et al. (1993) also referenced the conclusion of Jenkins et al. (1991) that metabolic rate responds differently to intake in breeds with differing maintenance requirements, and suggested that the extrapolation of those findings in application to within-breed variation would agree with their own results. Ultimately, Shuey et al. (1993) concluded that selecting for lower MEm would be an ineffective strategy for improving PE, provided that nutrition is not limiting relative to requirements. If, as may be the case in a nutritionally harsh environment, selection on MEm were desired, FHP would be an appropriate indicator trait (Shuey et al., 1993).

Utilizing Simmental X Angus, Charolais X Angus, Hereford X Angus, and Jersey X Angus, Bowden (1980) found no significant differences among these biological types for PE (digestible energy (DE) consumed per kg calf weaned). Green et al. (1991) found Bos indicus X Bos taurus dams to have significantly higher PE than Bos taurus X Bos taurus. However, increased heterosis of the Bos indicus-crossed cows must be considered, and would have been only accentuated by the use of quite aged cows in that study (Green et al., 1991). Freking and Marshall (1992) reported a negative association between milk production and PE (here, ME consumed by cow and calf / weaned calf weight; so, higher milk producers were
more efficient). However, the improvement in PE of these first-calf dams per unit milk increase grew smaller at increasing milk levels (Freking and Marshall, 1992). They found no relationship between PE and size of the heifers (Freking and Marshall, 1992). Butts et al. (1984) also found their measure of PE to be significantly related with milk production but not with initial cow weight in Angus pairs. Working with Hereford, Holstein, and Hereford X Holstein, Holloway et al. (1975b) found Holsteins to produce milk gross energy (GE) from feed DE more efficiently ($P < 0.01$), but Hereford dams’ progeny were significantly more efficient converters of both milk GE, and total DE from creep feed and milk combined, into weaning weight. Overall, they did not find significant differences in efficiency to weaning (kg calf weaned / Mcal DE consumed by cow and calf) (Holloway et al., 1975b). With Angus, Charolais, and reciprocal crosses of those two breeds, however, Marshall et al. (1976) found milk production differences to affect very significantly weaning weight and weaning efficiency (TDN consumed by cow and calf / calf weaning weight). Though cow weight significantly affected TDN consumption, it also had a significant effect on weaning weight (Marshall et al. 1976). It appeared that the increased energy consumption of heavier cows and their calves was effectively counterbalanced by heavier weaning weights; therefore, cow weight had a non-significant impact on weaning efficiency (Marshall et al., 1976). In that study, breed of dam significantly influenced both TDN consumption and cow weight, but had no significant relationship with milk production or weaning efficiency (Marshall et al., 1976). Using nine diverse beef breeds, Jenkins and Ferrell (1994) found that ranking for PE (weight of calf weaned/cow exposed/DMI of cow) varied at differing levels of DMI. Breeds with greater genetic potential for growth and(or) milk production were more efficient at the
higher intake levels (Jenkins and Ferrell, 1994). From their 1984 study, Ferrell and Jenkins suggested differences in PE among biological types. However, the estimated ME intake in their PE calculation was based upon an extrapolation (to 365 days) of the maintenance requirements determined in their study. They acknowledged the many other factors that can affect PE, such as ME required for pregnancy and lactation, non-milk ME intake by the calf, and any interactions among these variables (Ferrell and Jenkins, 1984).

One additional note regarding a possible relationship between dam milk production and PE concerns creep feeding. Calves had *ad libitum* access to creep feed in most of the PE studies reviewed here, and it would be reasonable to believe they consumed more energy than they likely would have from only pasture and milk. Although this intake was included in the PE calculations, it may have obfuscated the true relationship between milk production and PE in pasture-based, no-creep settings (Bowden, 1980; Brown and Dinkel, 1982; Marshall et al., 1976).

Any breeder deciding to pursue increased milking ability should bear in mind the potential detrimental effects on reproduction resulting from a level of milk production that cannot be supported by the nutritional environment (e.g., Holloway et al., 1975a). Reproductive efficiency is an extremely important component of overall beef production efficiency, and its impairment should be very carefully weighed against potential improvement in weaned calf weight per unit energy consumed. Interestingly though, Marshall et al. (1976) found Charolais dams—which had the numerically lowest milk production—to be significantly less fertile and wean significantly fewer calves than Angus or the crossbreds. Milk production explained little variation in rebreeding performance.
(Marshall et al., 1976). Additionally, Freking and Marshall (1992) reported no influence of milk production on the rebreeding performance as 2-year-old first-calvers. Furthermore, Montaño-Bermudez and Nielsen (1990) concluded from their investigations with Low-, Medium-, and High-milk groups that “with adequate availability of feed sources for beef production in the midwest U.S. cows of medium size can vary widely in milk they provide to their calves and still have comparable reproductive performance.” However, care should be taken not to extrapolate any of these results beyond the range of milk production levels observed in these experiments. There should exist an optimal milk level for a given environment, at which dam reproduction and calf growth would be most profitably balanced.

A more accurate depiction of PE should extend beyond weaning and encompass the calves’ post-weaning performance and ultimate carcass merit. Holloway et al. (1975b) found Hereford dams generally (in some measures, significantly) to be more efficient converters of DE consumed by cow and calf into carcass GE or into retail cuts, compared with Holstein and Hereford X Holstein dams. Brown and Dinkel (1982) examined potential differences among Angus, Charolais, and reciprocal cross dams in energy requirements (estimated TDN intake) per unit weaning weight, slaughter weight, or retail product yield. Although there were significant differences between breed groups for cow weight, annual cow TDN, milk production, calf pre-weaning and post-weaning TDN, and retail cut yield, none were detected for feed energy requirements per unit weaning weight or per unit retail product yield. However, for total TDN per unit slaughter weight, Angus cows and their calves were more efficient (Brown and Dinkel, 1982).
Summary

With such a large portion of the total feed consumed in beef production being used by the breeding cow herd, improving efficiency in this segment of the production cycle certainly demands attention. Studies involving maintenance efficiency have demonstrated that animals with greater milk production ability generally have increased maintenance requirements as well. Along with variation in fat deposition, this may be because relatively larger viscera and other internal “machinery” required to support heavy lactation need nutrients for maintenance even during non-lactation. Production efficiency investigations point toward heavier-milking cows as being most efficient, in terms of weight of calf weaned with calf and dam intake considered. Maintenance requirement appears to have little bearing on PE, at least in environments where nutrition is not limiting. Seedstock selected on PE in very favorable environments may not perform as well under more adverse conditions. Milk production must be kept at appropriate levels that allow satisfactory reproductive performance. Also, appropriate consideration must always be given to post-weaning calf performance and carcass traits.
Residual Feed Intake of Growing Beef Cattle

Interest in RFI appears to be on the rise. It may be the trait’s alleged independence of growth rate and size that makes it an attractive measure of efficiency. A brief introduction to RFI has already been provided. The following is a closer look at RFI and its relationship with other traits.

Test length

Having analyzed records of growing heifers and bulls of British beef breeds, Archer et al. (1997) determined that a 35-day test was adequate for feed intake measurement. However, a 70-day test was deemed necessary for accurate assessment of growth rate (and consequently also for efficiency traits that depend upon growth rate—e.g., FCR and RFI), assuming that animals are weighed bi-weekly (Archer et al., 1997). Wang et al. (2006) suggested that a 63-day test would be sufficient for determining RFI, provided that animals were weighed weekly.

Heritability of RFI

The original heritability estimate by Koch et al. (1963) of the trait to become known as RFI was $h^2 = 0.28 \pm 0.11$. That study involved 1,324 bull and heifer calves of British breeds, from 3 herds, sired by 120 bulls. Arthur et al. (2001a) analyzed the records of 1,180 Angus bulls and heifers and reported a heritability estimate of $h^2 = 0.39 \pm 0.03$. Herd and Bishop (2000) estimated the heritability of RFI measured in Hereford bull calves ($n = 540; 154$ sires) to be $h^2 = 0.16 \pm 0.08$. In Charolais bulls ($n = 792; 80$ sires), Arthur et al. (2001b)
reported $h^2 = 0.39 \pm 0.04$. Schenkel et al. (2004) found the heritability of RFI to be $h^2 = 0.38$ in growing beef bulls. Data were obtained from bull test stations, with feed intake records available for 2,284 bulls of 6 breeds (888 sires) (Schenkel et al., 2004). From records of 1,481 steers and heifers (some Bos indicus-influenced), Robinson and Oddy (2004) reported RFI heritability of $h^2 = 0.21 \pm 0.12$. Nkrumah et al. (2007b), working with steers (n = 464) from Alberta Hybrid cows and sired by Angus, Charolais, or Alberta Hybrid bulls (28 sires), found $h^2 = 0.21 \pm 0.12$. Elzo et al. (2009), whose study included calves (n = 581) of Bos indicus breeding, reported an RFI heritability of $h^2 = 0.19 \pm 0.11$ in their population. Bouquet et al. (2010) found heritability of RFI to be $h^2 = 0.26$ and $h^2 = 0.45$ from their Blonde d’Aquitaine (n = 678) and Limousin (n = 708) bull records, respectively. Working with Brangus heifers (n = 468; 36 sires), Lancaster et al. (2009b) reported $h^2 = 0.47 \pm 0.13$. From records of Irish performance-tested beef bulls (n = 2,605), Crowley et al. (2010) estimated direct heritability of RFI to be $h^2 = 0.45 \pm 0.06$. After significantly improving model fit by considering maternal genetic variance, Crowley et al. (2010) reported $h^2_D = 0.37 \pm 0.07$ and $h^2_M = 0.09 \pm 0.04$, with a correlation between direct and maternal components of $r = 0.82 \pm 0.82$. From records of 514 Japanese Black bulls, Hoque et al. (2009) found direct $h^2 = 0.51 \pm 0.04$. After including maternal effects, they reported $h^2_D = 0.35 \pm 0.05$ and $h^2_M = 0.24 \pm 0.03$, with direct-maternal correlation of $r = 0.06 \pm 0.03$ (Hoque et al., 2009).

**Relationship of RFI with intake and other measures of feed utilization**

Arthur et al. (2001a) reported the phenotypic and genetic correlations between RFI and daily feed intake to be $r_p = 0.72$ and $r_g = 0.69 \pm 0.03$, respectively. Herd and Bishop
(2000) likewise observed correlations between RFI and intake ($r_p = 0.70 \pm 0.02; r_g = 0.64 \pm 0.16$). In 15-month-old Charolais bulls, Arthur et al. (2001b) also found RFI and intake to be significantly correlated ($r_p = 0.60$ and $r_g = 0.79 \pm 0.04$). Elzo et al. (2009) also reported a significant correlation of RFI with intake ($r_p = 0.89 \pm 0.01$ and $r_g = 0.73 \pm 0.13$). Nkrumah et al. (2007b), too, found strong correlations between daily dry matter intake and RFI ($r_p = 0.64; r_g = 0.73 \pm 0.18$). Lancaster et al. (2009b) also reported very strong correlations between intake and RFI in Brangus heifers ($r_p = 0.70; r_g = 0.85 \pm 0.08$). Working with Japanese Black (Wagyu) bulls, Hoque et al. (2006) found correlations between RFI and intake of $r_p = 0.72$ and $r_g = 0.78 \pm 0.06$.

In Angus steers, Baker et al. (2006) found RFI to be positively phenotypically correlated with FCR ($r = 0.42$). Herd and Bishop (2000), working with Hereford bull calves, reported FCR and RFI to be phenotypically and genetically correlated ($r_p = 0.61 \pm 0.03; r_g = 0.70 \pm 0.22$). Correlations with RFI were similar ($r_p = 0.63 \pm 0.03; r_g = 0.72 \pm 0.18$) when Herd and Bishop (2000) analyzed lean feed conversion ratio (LFCR; feed intake / (weight gain X predicted carcass lean proportion)). Arthur et al. (2001a) found RFI and FCR to be correlated ($r_p = 0.53; r_g = 0.66 \pm 0.05$). Having analyzed performance records of bulls of 6 beef breeds developed on central tests, Schenkel et al. (2004) reported phenotypic and genetic correlations between FCR and RFI of $r_p = 0.76$ and $r_g = 0.69$. When backfat was also included in the multiple regression to predict feed intake (versus MetMW and ADG alone), this RFI$_b$ was similarly correlated with FCR ($r_p = 0.74; r_g = 0.68$) (Schenkel et al., 2004). In growing Angus bulls, Lancaster et al. (2009a) found RFI and RFI$_c$ (for which gain in 12$^{th}$-rib backfat and in LM area were included in the predicted DMI model) to be phenotypically
correlated with FCR ($r = 0.49$ and $r = 0.45$, respectively). With Brangus heifers, Lancaster et al. (2009b) reported RFI and $RFI_c$ (here including gain in backfat and final LM area) to be correlated with FCR ($r_p = 0.59$ and $r_p = 0.56$, respectively). They also reported very strong genetic correlations of RFI and $RFI_c$ with FCR of $r_g = 0.93 \pm 0.09$ and $r_g = 0.94 \pm 0.09$, respectively (Lancaster et al., 2009b). In crossbred cattle (predominantly steers but also a small proportion of bulls), Nkrumah et al. (2004) also observed a phenotypic correlation between FCR and RFI ($r = 0.62$). From a similar dataset, Nkrumah et al. (2007b) reported phenotypic and genetic relationships between RFI and FCR of $r_p = 0.52$ and $r_g = 0.62 \pm 0.09$. Arthur et al. (2001b) reported correlations of RFI with FCR ($r_p = 0.57; r_g = 0.85 \pm 0.05$) in Charolais bulls. Hoque et al. (2006) found strong correlations between RFI and FCR of $r_p = 0.76$ and $r_g = 0.64 \pm 0.10$. Elzo et al. (2009) detected a phenotypic correlation between RFI and FCR ($r_p = 0.55 \pm 0.03$), but surprisingly no significant genetic relationship between RFI and FCR ($r_g = 0.09 \pm 0.38$). Bouquet et al. (2010) found genetic correlations of RFI and FCR to be $r_g = 0.72 \pm 0.22$ and $r_g = 0.37 \pm 0.25$ in Blonde d’Aquitaine and Limousin bulls, respectively. Crowley et al. (2010) reported correlations between RFI and FCR of $r_p = 0.41; r_g = 0.48 \pm 0.10$.

Lancaster et al. (2009a) calculated partial efficiency of growth (PEG) as the ratio of ADG to DMI used for growth. To compute DMI used for maintenance (which was subsequently subtracted from total DMI to find that portion for growth), they multiplied MBW by 0.077 and then divided by the $NE_m$ concentration of the ration, as outlined by the NRC (2000). They found PEG to be negatively phenotypically correlated with RFI ($r_p = -0.84$) and $RFI_c$ ($r_p = -0.78$) (Lancaster et al., 2009a). Nkrumah et al. (2007b) also determined
PEG this way, and also reported strong correlations of RFI with PEG ($r_p = -0.83$; $r_g = -0.87 \pm 0.06$). Likewise, Hennessy and Arthur (2004) observed a phenotypic correlation of $r_p = -0.79$ between PEG and RFI in Hereford steers and heifers. In Charolais bulls, Arthur et al. (2001b) also reported correlations between RFI and PEG ($r_p = -0.65$; $r_g = -0.94 \pm 0.02$). The strength of these relationships is not unexpected, considering that PEG and RFI each include ADG and maintenance requirement estimates in their measure of feed utilization efficiency (Nkrumah et al., 2004).

Herd and Bishop (2000) used allometric equations involving protein and fat accretion and assumed standard efficiencies for their deposition to calculate ME required for growth (DEP). Correlations between RFI and DEP were statistically non-significant ($r_p = 0.06 \pm 0.04$; $r_g = 0.27 \pm 0.30$). Herd and Bishop (2000) also defined maintenance energy expenditure (MAINT) as the difference between ME intake and calculated DEP. MAINT and RFI were correlated ($r_p = 0.78 \pm 0.02$; $r_g = 0.77 \pm 0.13$). Correlations with RFI were even stronger when maintenance energy expenditure was expressed on MBW basis (MMBW; MAINT/MBW) ($r_p = 0.91 \pm 0.01$; $r_g = 0.93 \pm 0.06$).

Relationship of RFI with growth rate and size

As indicated previously, RFI would not be correlated with traits used in the regression to predict intake. In many studies, intake has been predicted by phenotypic multiple regression on MetMW and ADG; therefore, the absence of phenotypic association between RFI and these traits is commonly reported and will not be noted here.

Most studies where animals have been classified into RFI groups have found similar
performance (BW, ADG) between groups, with low-RFI animals eating less (Richardson et al., 2001; Nkrumah et al., 2004; Castro Bulle et al., 2007; Bingham et al., 2009; Lancaster et al., 2009a; Lancaster et al., 2009b; Crowley et al., 2010). However, Elzo et al. (2009), working with steers, heifers, and bulls that were Angus, Brahman, and crosses (varying proportions) of these breeds, found their high-RFI group (calf RFI > mean RFI + 0.5 SD) actually to show a significantly greater post-weaning gain than the low-RFI group (calf RFI < mean RFI - 0.5 SD). As would be expected, the high-RFI group also consumed significantly more DM to achieve their gains (Elzo et al., 2009). This finding may be related to that fact that the low-RFI group contained significantly more influence from Brahman, which in that study exhibited significantly lower RFI but also significantly lower post-weaning gain.

Nkrumah et al. (2004) found RFI to be phenotypically independent of both relative growth rate (RGR; growth relative to instantaneous body size) and Kleiber ratio (ADG / MetMW). Hennessy and Arthur (2004) also observed RFI to be phenotypically independent of RGR and Kleiber ratio, as did Arthur et al. (2001b) in Charolais bulls. These findings are not surprising, given the inclusion of gain rate (ADG) and size (MetMW) in the DMI prediction equation for RFI. However, Arthur et al. (2001b) also reported significant negative genetic correlations of RFI with RGR ($r_g = -0.56 \pm 0.12$) and Kleiber ratio ($r_g = -0.40 \pm 0.13$). Crowley et al. (2010) found RFI to be phenotypically independent of RGR and Kleiber ratio. The genetic correlations of RFI with RGR and Kleiber ratio were positive, but not significantly different from zero ($r_g = 0.21 \pm 0.12$ and $r_g = 0.15 \pm 0.13$, respectively) (Crowley et al., 2010).

In addition to phenotypic independence, Arthur et al. (2001a) found no genetic
relationship between RFI and ADG in their Angus population ($r_g = -0.04 \pm 0.08$). They did observe genetic correlations of RFI with direct effects for 200-d weight ($r_g = -0.45 \pm 0.17$) and 400-d weight ($r_g = -0.26 \pm 0.13$) (Arthur et al., 2001a). Herd and Bishop (2000) also reported RFI to be genetically independent of ADG ($r_g = 0.09 \pm 0.29$). While still not statistically different from zero, genetic correlations of RFI with 200-d weight ($r_g = 0.34 \pm 0.34$), 400-d weight ($r_g = 0.15 \pm 0.28$), and MetMW ($r_g = 0.22 \pm 0.29$) were relatively greater (Herd and Bishop, 2000). Similarly, Lancaster et al. (2009b) observed no genetic correlation between RFI and ADG ($r_g = 0.04 \pm 0.32$), but reported a larger—yet still not significant—correlation of RFI with MetMW ($r_g = 0.33 \pm 0.29$). In Charolais bulls, Arthur et al. (2001b) observed a positive genetic correlation of RFI with liveweight ($r_g = 0.32 \pm 0.10$), while RFI’s genetic relationship with ADG failed to reach significance. ($r_g = -0.10 \pm 0.13$). With Irish beef bulls, Crowley et al. (2010) also reported genetic independence between RFI and ADG. The genetic correlation between RFI and MetMW was negative ($r_g = -0.17 \pm 0.09$) (Crowley et al., 2010). In growing dairy bulls, Jensen et al. (1992) also found the genetic correlation between RFI and ADG to be statistically non-significant. Schenkel et al. (2004) found no significant genetic correlations between ADG and RFI or RFIb in young beef bulls. Robinson and Oddy (2004) also reported no significant genetic correlations of RFI with ADG or weight. Genetic correlations of RFI with ADG (0.25 ± 0.16) and MetMW (0.16 ± 0.13) reported by Hoque et al. (2006) were not significantly different from zero. Herd and Bishop (2000) found lean growth rate (LGR; growth rate to 400 d X predicted carcass lean content) to be phenotypically and genetically correlated with RFI ($r_p = -0.33 \pm 0.04; r_g = -0.47 \pm 0.17$). Bouquet et al. (2010) reported RFI and liveweight (adjusted to 450 days) to be negatively
correlated ($r_g = -0.40 \pm 0.21$) in Blonde d’Aquitaine bulls. However, that association was not significant in their Limousin population ($r_g = -0.07 \pm 0.14$) (Bouquet et al., 2010). Elzo et al. (2009), with Angus, Brahman, and crosses as described previously, reported a genetic correlation between RFI and post-weaning gain (i.e., ADG) of $r_g = 0.58 \pm 0.28$. That finding would not be favorable for an industry that desires both rapid weight gain and efficiency (as measured by RFI).

Schenkel et al. (2004) reported no significant correlations of RFI or RFI$_b$ with hip height of bulls, measured at completion of centralized performance tests. Nkrumah et al. (2004) similarly found RFI to be independent of hip height in hybrid steers and bulls. Basarab et al. (2003) also observed no significant phenotypic correlation of RFI with hip height or with gain in hip height in crossbred beef steers.

Herd and Bishop (2000) also analyzed the relationships of performance and efficiency traits of progeny with the mature size of their dams. Weight (COWWT) was recorded for each dam at an age of approximately 4.5 years. RFI of the progeny was determined to be genetically independent of COWWT ($r_g = -0.09 \pm 0.26$).

Relationship of RFI with body composition and carcass traits

Ultrasound fat measurements

Baker et al. (2006) found no significant phenotypic correlations between RFI and ultrasonic measurements of backfat thickness (RpFt), scanned at both the initiation and the completion of the 70-d test. Schenkel et al. (2004) reported a phenotypic correlation between RFI and RpFt of $r_p = 0.17$, while the genetic correlation (0.16) failed to reach significance at
the \( \alpha = 0.05 \) level. When they included RpFt in the intake model, the phenotypic and genetic correlations of RFI with RpFt, each fell, understandably, to -0.01 (Schenkel et al., 2004).

Lancaster et al. (2009a) observed phenotypic correlations of RFI with gain in RpFt \( (r_p = 0.30) \) and with final RpFt \( (r_p = 0.20) \). Nkrumah et al. (2004) also found RFI to be phenotypically correlated with RpFt \( (r_p = 0.19) \) and with gain in RpFt during the test period \( (r_p = 0.30) \). Basarab et al. (2003) reported a phenotypic relationship of RFI with RpFt approaching significance \( (r_p = 0.15; P = 0.07) \), as well as a significant correlation of RFI with gain in RpFt \( (r_p = 0.22) \). In Brangus heifers, Lancaster et al. (2009b) found RFI to be significantly phenotypically correlated with final RpFt \( (r_p = 0.12) \), as well as gain in RpFt \( (r_p = 0.22) \). They also reported a genetic correlation between RFI and final RpFt of \( r_g = 0.36 \pm 0.26 \) (Lancaster et al., 2009b). In Angus cattle, Arthur et al. (2001a) found RFI to be correlated with ultrasound rib fat \( (RbFt) \) \( (r_p= 0.14; r_g = 0.17 \pm 0.05) \). The association of RFI with RpFt at the P8 site did not reach significance in that study \( (r_p = 0.11; r_g = 0.06 \pm 0.06) \) (Arthur et al., 2001a). Robinson and Oddy (2004) reported strong correlations of RFI with \( RbFt \) \( (r_g = 0.48 \pm 0.12) \) and P8 \( RpFt \) \( (r_g = 0.72 \pm 0.17) \). When these ultrasound fat measurements were adjusted to a constant carcass weight—rather than age—the correlations rose to \( r_g = 0.58 \pm 0.14 \) and \( r_g = 0.79 \pm 0.16 \), respectively (Robinson and Oddy, 2004). Herd and Bishop (2000) predicted lean carcass content \( (LEAN) \) from RpFt measurements. They reported phenotypic and genetic correlations of RFI with \( LEAN \) of \( r_p = -0.22 \pm 0.04 \) and \( r_g = -0.43 \pm 0.23 \). In Angus steer progeny from lines divergently selected for RFI (single generation), Richardson et al. (2001) did not find a significant correlation of sire’s estimated breeding value \( (EBV) \) for RFI with progeny ultrasound fat thickness at either the rib or P8
rump site. Nor was there a significant difference between groups (Richardson et al., 2001).

Schenkel et al. (2004) found no significant correlations between ultrasound estimate of intramuscular fat percentage (ulMF) and either RFI or RFIb in bulls. Lancaster et al. (2009a) likewise reported no significant phenotypic correlations of either RFI or RFIc with either ulMF or gain in ulMF during the trial. Nkrumah et al. (2004) also observed RFI to be independent of ultrasound-based marbling score in crossbred steers and bulls. While Basarab et al. (2003) found no significant phenotypic relationship of RFI with either initial or final ultrasound marbling score, RFI was significantly correlated with gain in ultrasound marbling score ($r_p = 0.22$). Lancaster et al. (2009b) found no significant correlations—phenotypic or genetic—of RFI or RFIc with final ulMF, or with gain in ulMF. Richardson et al. (2001) did not find a significant correlation between ulMF and sire’s EBV for RFI.

Ultrasound ribeye area

Baker et al. (2006) found no significant phenotypic correlations between RFI and ultrasound measurements of ribeye (*longissimus dorsi*) area (REA), collected at both the beginning and completion of the 70-day test. Schenkel et al. (2004) reported no significant correlations of REA with RFI or RFIb in growing beef bulls. Nkrumah et al. (2004) reported no significant relationship between RFI and REA. Basarab et al. (2003) also found RFI to be phenotypically independent of both REA and gain in REA. Lancaster et al. (2009a) observed a significant phenotypic correlation of RFI with gain in REA ($r_p = 0.17$), but not with final REA ($r_p = 0.09$). Working with Angus bulls and heifers, Arthur et al. (2001a) found the relationship (phenotypic and genetic) of RFI with REA to be non-significant. In Brangus
heifers, Lancaster et al. (2009b) reported phenotypic correlations of RFI with final REA or gain in REA to be non-significant. The genetic correlation of RFI with final REA was also near zero, while RFI and gain in REA showed a much stronger genetic relationship ($r_g = 0.55 \pm 0.24$) (Lancaster et al., 2009b). Robinson and Oddy (2004) reported a significant, positive phenotypic correlation between RFI and REA ($r_p = 0.17$), while the genetic correlation ($r_g = -0.24 \pm 0.26$) was negative but not significantly different from zero.

Carcass traits

With carcasses from Angus steers classified as high (> 0.5 SD above mean), medium (± 0.5 SD from mean), or low (< 0.5 SD below mean) RFI, Baker et al. (2006) detected no differences among RFI groups for hot carcass weight. Nkrumah et al. (2004) also observed RFI to be phenotypically independent of cold carcass weight in crossbred steers. Basarab et al. (2003) also did not observe a significant phenotypic correlation between RFI and carcass weight.

Baker et al. (2006) found no significant differences among RFI groups for backfat thickness; kidney, pelvic, and heart fat (KPH); or USDA Yield Grade. In crossbred beef steers, Mader et al. (2009) reported phenotypic correlations of RFI ($r_p = 0.34$) and RFI$_b$ ($r_p = 0.29$) with trim and kidney fat weight proportion, but not with any other fat-related traits in their study. Nkrumah et al. (2004) observed phenotypic correlations of RFI with carcass grade fat ($r_p = 0.25$), Canadian yield grade ($r_p = 0.28$), and lean meat yield ($r_p = -0.22$). From their serial slaughter experiment with crossbred beef steers, Basarab et al. (2003) reported a relationship between RFI and estimated gain in empty-body fat, expressed in either absolute
terms (g/d) \( (r_p = 0.26) \) or relative to MBW (g/kg MBW/d) \( (r_p = 0.30) \). They also reported a phenotypic correlation between RFI and dissectible carcass lean \( (r_p = -0.21) \). Additionally, Basarab et al. (2003) observed that RFI tended to be positively associated with dissectible carcass fat \( (r_p = 0.14; P < 0.09) \).

Baker et al. (2006) did not find differences among RFI groups for marbling score or for USDA Quality Grade. Nkrumah et al. (2004) similarly found no significant phenotypic correlation between RFI and carcass marbling score in crossbred steers. Basarab et al. (2003) reported that RFI trended toward association with carcass marbling \( (r_p = 0.15; P = 0.07) \). Robinson and Oddy (2004) observed a relatively weak but significant phenotypic correlation \( (r_p = 0.11) \) between RFI and carcass percentage intramuscular fat, while the genetic correlation \( (r_g = 0.22 \pm 0.17) \) was not different from zero.

Nkrumah et al. (2004) reported no significant phenotypic correlation between RFI and carcass ribeye area. Basarab et al. (2003) also found RFI to be phenotypically independent of carcass ribeye area. Baker et al. (2006) observed no significant differences among RFI groups for carcass ribeye area.

Meat quality

Baker et al. (2006) examined the relationship between RFI and measures of meat quality and palatability in Angus steers. By proximate analysis, steaks from medium-RFI steers tended \( (P < 0.10) \) to contain more protein than those of low-RFI steers, and less lipid and more moisture than those from high-RFI. There were no significant differences across the RFI groups for L* or a* reflectance color values. However, high-RFI steers produced
steaks with significantly greater b* values, compared with those from medium- and low-RFI steers. Calpastatin activity did not differ between high- and low-RFI groups (medium-RFI group was not evaluated). Steaks had significantly lower cooking loss from medium- versus low-RFI steers. Warner-Bratzler shear force measurements were similar among the groups, and there was no RFI group by postmortem aging period interaction. A 9-member trained sensory panel also evaluated steaks from steers of the RFI groups. The findings of this panel showed no differences among RFI groups for ratings of tenderness or intensity of flavor. However, steaks from high-RFI steers tended (P < 0.10) to be less juicy versus medium- or low-RFI steaks, and also had significantly less off-flavor than those from the low-RFI group. It should be noted that the maximum off-flavor score detected was 1.2 (on a 10-point scale), and was not considered to be detrimental to eating quality (Baker et al., 2006). Overall, Baker et al. (2006) concluded that meat quality and palatability were not different between high- and low-RFI Angus steers, but they encouraged continued monitoring for any correlated responses, due to the present lack of understanding regarding the biological basis of RFI and incomplete awareness of its potential genetic associations with meat quality traits.

McDonagh et al. (2001) investigated effects on meat quality after divergent selection on RFI. Meat from steers of the High- and Low-efficiency lines had similar meat color, fat color, shear force, and compression values. Differences were found in calpastatin and in myofibril fragmentation index (MFI) values, both suggesting that selection for improved RFI could negatively affect meat quality.
Relationship of RFI with behavioral traits

Feeding behavior

Several studies have investigated relationships between RFI and feeding behavior traits, and the potential use of such traits as indicators of intake or efficiency. The advent of radio frequency identification technology and its utilization in the GrowSafe® automated data acquisition system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) has enabled such eating behavior traits—along with intake—to be measured much more conveniently. However, when a GrowSafe® system is not available, one alternative is the use of video surveillance in conjunction with Calan® gates (American Calan, Northwood, NH) (Bingham et al., 2009).

In feeding behavior studies, a meal event is typically defined as beginning when an animal’s transponder is first detected and ending when the period between the last 2 transponder readings is greater than 300 seconds (e.g., Nkrumah et al., 2007a). A meal could also terminate before that period has elapsed if another animal’s transponder is detected at that bunk or that animal’s transponder is detected at a different bunk. One feeding behavior trait commonly measured is meal frequency (MFREQ; events/d), which is simply the number of independent feeding events recorded for an animal in a day. Significant phenotypic correlations of MFREQ with RFI have been reported (Robinson and Oddy, 2004; Nkrumah et al., 2007a; Lancaster et al., 2009) and range from $r_p = 0.18$ to $r_p = 0.26$. Two estimates of the genetic correlations between RFI and MFREQ were found and are quite distinct (Nkrumah et al., 2007a—$r_g = -0.34 \pm 0.30$; Robinson and Oddy, 2004—$r_g = 0.43 \pm 0.11$).

Another frequently investigated feeding behavior trait is meal duration (MDUR;
min/d), which is the sum of the lengths of all daily individual meal events. Correlations of MDUR with RFI have ranged from $r_p = 0.16$ and $r_g = -0.35 \pm 0.17$ (Robinson and Oddy, 2004) to $r_p = 0.49$ and $r_g = 0.57 \pm 0.28$ (Nkrumah et al., 2007a). Lancaster et al. (2009a) also reported $r_p = 0.41$ for the correlation of MDUR with RFI in their Angus bulls. However, Bingham et al. (2009) did not detect a difference in MDUR between low-RFI and high-RFI groups of Brangus heifers.

A related trait often evaluated is head-down duration (HDUR; min/d), which is the number of times an animal’s transponder is detected each day multiplied by the scanning frequency of the specific GrowSafe system used in the study (scanning frequencies may range from 1.0 to 6.3 s (Nkrumah et al., 2007a)). HDUR is thus a more accurate estimate of the time during which an animal actually has its head in the bunk and is presumably consuming or masticating feed; MDUR may include time spent away from the bunk, so long as the animal returns within 5 minutes. Estimates of the relationship between HDUR and RFI have been reported by Lancaster et al. (2009a; $r_p = 0.38$) and Nkrumah et al. (2007a; $r_p = 0.50$ and $r_g = 0.33 \pm 0.30$). Bingham et al. (2009) observed a significant difference in HDUR between high-RFI and low-RFI heifers (greater HDUR for low-RFI group).

Meal-eating rate (MRATE; g/min), another feeding behavior trait, is calculated by dividing DMI by MDUR. The correlation between MRATE and RFI reported by Lancaster et al. (2009a) of $r_p = 0.08$ was not different from zero (at $\alpha = 0.05$). Bingham et al. (2009), however, did observe a highly significant difference in MRATE between RFI groups (lower MRATE for low-RFI heifers).
Exit velocity and temperament score

Exit velocity (EV), also known as flight speed (FS), is a measure of the speed with which an animal traverses a specified distance (1.7, 1.83, or 2.44 m in the studies reviewed here) upon release from a chute, such as after processing (Curley et al., 2006). Burrow (2001) reported that EV was heritable ($h^2 = 0.40 – 0.44$) in a tropically adapted cattle population. Temperament scoring is another method of evaluating an animal’s disposition and excitability. These subjective scores are based on a 1-5 (Curley et al., 2006) or a 1-6 scale (BIF, 2002; Elzo et al., 2009), with 1-scored animals being very calm and higher-scoring animals being progressively more agitated or aggressive. Such scoring often takes place while the animal is confined—but not fully restrained—in a chute (chute score; CS), but pen scores (PS) may also be issued to animals evaluated in a small group within a pen (Curley et al., 2006).

Exit velocity has been shown to be associated with growth rate, such that calmer, more slowly moving cattle gain better (Burrow and Dillon, 1997; Voisinet et al., 1997b). Additionally, high chute score has been linked with a detrimental effect on tenderness and incidence of “dark cutters” (Voisinet et al., 1997a; Kadel et al., 2006). A potential relationship of temperament traits with feed utilization efficiency has also been investigated.

Elzo et al. (2009) found no significant correlation of either mean EV or mean CS (average of 6 velocities or scores, respectively) with FCR or RFI. Exit velocity was significantly correlated with daily feed intake, such that calves that ate more exited the chute more slowly. The authors pointed out that while this may indicate the influence of temperament on intake, it may also simply be that calves that ate more moved more
sluggishly due to their fullness. Elzo et al. (2009) failed to detect a significant relationship of EV or CS with ADG during the 70-d trial. Regarding the absence of correlation with temperament traits (other than EV with intake), the authors noted that the calves were worked through the chute relatively frequently, likely became accustomed to that type of handling, and thus variation in behavioral traits among the calves may have decreased (Elzo et al., 2009).

Nkrumah et al. (2007a) also reported a significant phenotypic relationship of EV with DMI ($r_p = -0.35$; $r_g = -0.11 \pm 0.26$). Exit velocity was phenotypically independent of FCR and RFI, and genetic correlations of EV with FCR and RFI were $r_g = 0.40 \pm 0.26$, and $r_g = -0.59 \pm 0.45$, respectively. Exit velocity was correlated with ADG ($r_p = -0.26$; $r_g = -0.25 \pm 0.25$). A relationship between EV and PEG was also observed ($r_p = -0.13$; $r_g = 0.72 \pm 0.19$). Additionally, Nkrumah et al. (2007a) also found EV to be phenotypically independent of RpFt, significantly correlated (phenotypically and genetically) with REA, and independent of uIMF. Exit velocity was negatively correlated with carcass weight and with carcass grade fat, and positively with carcass ribeye area and lean meat yield. Exit velocity was negatively phenotypically correlated with carcass marbling score (Nkrumah et al., 2007a).

**Relationship of RFI in growing stage with RFI at maturity**

To date, there is relatively little published work regarding any relationship between efficiency in growing heifers and their efficiency later in life as mature, producing cows. The subject is tremendously important for understanding the response in the breeding herd due to selection during the growth phase, and deserves further exploration.
Archer et al. (2002) measured feed intake, BW gain, and other traits of 751 beef cows (of British breeds) that had previously undergone similar testing as heifers in the post-weaning stage. Following weaning of their second calf, the cows had *ad libitum* access to a pelleted feed (approximately 10 MJ ME/kg dm and 17% protein) for a 70-d test, following a 14-d to 21-d acclimation period. Heritability of RFI (intake predicted by regression on MetMW and ADG) in these cows was estimated to be $h^2 = 0.23$. Residual feed intake in the cows was reported to be correlated with their RFI as post-weaning heifers ($r_p = 0.40; r_g = 0.98$). Measurements of FCR at the two ages were not as strongly correlated ($r_p = 0.10; r_g = 0.20$). It is important to note that these cows were neither gestating nor lactating, and also such a ration is not commonly encountered on commercial beef operations. These points may seriously impact the extrapolation of these results to typical forage-based production systems (Archer et al., 2002). However, these limited results do indicate that selection based on post-weaning RFI should yield a strong correlated response in RFI at maturity.

Additionally, Nieuwhof et al. (1992) reported RFI in post-weaning dairy heifers to be genetically correlated ($r_g = 0.58$) with RFI during first lactation. Working with mice, Archer et al. (1998) observed correlations ($r_p = 0.29; r_g = 0.60$) between post-weaning RFI and RFI at maturity.

*Relationship of RFI with dam productivity traits*

Basarab et al. (2007) examined the relationship between progeny RFI and measures of productivity of the dams. With calves grouped by RFI_b (includes adjustment for backfat; Low = < 0.5 below mean RFI_b; Medium = ± 0.5 SD; High > 0.5 SD), there were no
significant differences in pregnancy, calving, or weaning rates among dams of Low, Medium, or High progeny. However, dams of High calves did exhibit a higher twinning rate (P < 0.001) and tended to have increased calf death loss (P = 0.10). Calf birth weight, pre-weaning ADG, 200-d weight, cow production efficiency (here, (calf weaning weight / dam weight at weaning) X 100), and cow weight were not significantly different among groups. Interestingly, dams of Low progeny were reported to consistently have greater backfat thickness and to lose less weight than dams of High RFIb progeny. A significant interaction with age was also present, with backfat differences among RFIb groups widening with increasing age of the dams. Calving interval did not differ among groups; however, dams of Low progeny did calve 5-6 days later in the season (P < 0.001). Subsets of mature dams from each group entered a feeding trial after weaning, during the second trimester of gestation. Dams of Low and Medium calves had significantly lower DMI and RFI during this period than did dams of High progeny (Basarab et al., 2007).

Arthur et al. (2005) looked at the effects on maternal productivity in Angus cows following divergent selection for post-weaning RFI. The sample had experienced an average of 1.5 generations of selection, resulting in a difference of 0.8 kg/d in estimated breeding value for RFI. No significant differences were found between selection lines for pregnancy, calving, or weaning rates; milk yield; or weight of calf weaned per exposed cow. However, these authors also observed a trend (P = 0.07) toward later calving date (mean of 5 days) in the Low-RFI line. They called for future work with RFI-evaluated females to include investigation of age at puberty or time required for return to estrous activity following calving (Arthur et al., 2005).
Additionally, McDonald and Nielsen (2007), working with mice divergently selected on heat loss, observed that the Low maintenance requirement (or, Low heat loss) line, which ate the least, had significantly smaller litters than control or High lines. The High line, however, interestingly showed a nearly significant ($P = 0.08$) reduction in conception rate, compared with that of the Low line (control and Low conception rates were nearly identical) (McDonald and Nielsen, 2007).

*Computing RFI from expected requirements*

Residual feed intake described thus far in this review has referred to that for which intake is predicted by linear regression using the experimental data. However, an alternative method of calculating expected intake involves applying formulae from sources such as the National Research Council’s *Nutrient Requirements of Beef Cattle* (NRC, 1984; 2000), for example. These formulae provide standard values of energy requirements for maintenance and for weight gain. Having used such a method to predict intake of Angus and Hereford growing bulls, Fan et al. (1995) reported a heritability estimate of $h^2 = 0.14 \pm 0.12$. They found negative phenotypic and genetic correlations of this RFI with ADG and yearling weight. This RFI was also very strongly, negatively correlated with gross efficiency (defined there as ADG/MEI) (Fan et al., 1995). While RFI by regression using the dataset should have a mean very near zero, the RFI values (by NRC requirements) reported by Fan et al. (1995) for the 3 trial years had means of $-1.30 \pm 0.10$, $-0.76 \pm 0.10$, and $0.11 \pm 0.10$ (Mcal of ME/d).

Hennessy and Arthur (2004) computed RFI by both approaches for their experiment
involving Hereford steers and heifers. Residual feed intake calculated after predicting intake with an equation (SCA, 1990) using BW and expected mature BW was phenotypically correlated ($r_p = 0.62$) with RFI (intake predicted by regression on ADG and MetMW). The alternative RFI was not significantly phenotypically correlated with FCR, but was found to be correlated with intake ($0.88$), PEG ($-0.64$), RGR ($0.27$), Kleiber ratio ($0.37$), and ADG ($0.67$). Means for the alternative RFI in this study were also negative and different from zero (indicating that predicted intake was, on average, overestimated) (Hennessy and Arthur, 2004).

Arthur et al. (2001b) also calculated RFI by both methods (feeding standards formulae for that approach were obtained from Geay and Micol, 1988). In Charolais bulls, they found the two RFI traits to be correlated ($r_p = 0.70; r_g = 0.89 \pm 0.02$). Additionally, the alternative RFI was correlated with intake ($r_p = 0.49; r_g = 0.50 \pm 0.07$), FCR ($r_p = 0.84; r_g = 0.93 \pm 0.02$), PEG ($r_p = -0.66; r_g = -0.81 \pm 0.04$), RGR ($r_p = -0.23; r_g = -0.77 \pm 0.08$), Kleiber ratio ($r_p = -0.27; r_g = 0.40 \pm 0.14$), and ADG ($r_p = 0.38; r_g = -0.54 \pm 0.09$). Their standards also resulted in a negative mean for the alternative RFI (Arthur et al., 2001b).

Robinson and Oddy (2004), also included both types of RFI for their animals (some of which were *Bos indicus*-influenced), with the alternative method employing the equation from SCA (1990). They reported the two RFI traits to be highly correlated ($r_p = 0.94; r_g = 0.98 \pm 0.03$). The alternative version of RFI was heritable ($h^2 = 0.13 \pm 0.05$) and correlated with intake ($r_p = 0.42; r_g = 0.32 \pm 0.20$) and FCR ($r_p = 0.63; r_g = 0.69 \pm 0.27$) (Robinson and Oddy, 2004).
Physiological basis of RFI

Archer et al. (1999) outlined three major motivations for understanding the biological basis of variation in feed efficiency. One reason is that knowledge of this basis should provide insight for predicting possible correlated responses to selection for improved feed efficiency. This should be helpful in directing research into correlated responses. Secondly, an understanding of the physiological basis could assist in identification of indicator traits that can be measured more easily and less expensively than feed intake and efficiency. Such traits could be incorporated into selection programs for improved feed efficiency. Finally, understanding the physiological basis of variation in feed efficiency could result in development of alternative methods of manipulating metabolism. Feed efficiency in beef cattle could thus be improved by non-genetic means (Archer et al., 1999).

While the underlying biological causes of variation in RFI are—at present—far from perfectly understood, Herd and Arthur (2009) identified five major sources contributing to variation in RFI. These are intake of feed, digestion of feed, metabolism, activity, and thermoregulation. Richardson and Herd (2004), working with divergently selected Angus populations, determined that protein turnover, tissue metabolism, and stress accounted for 37% of the variation in RFI, while other identified contributors included digestibility (10%), heat increment and fermentation (9%), physical activity (9%), body composition (5%), and feeding patterns (2%). Nkrumah et al. (2006) helped elucidate the relationship of RFI with heat production and with methane emission (see also Hegarty et al., 2007). Kolath et al. (2006) and Bottje and Carstens (2009) have explored the association between mitochondrial function and RFI. The role of IGF-1 has also been investigated (Moore et al., 2005).
While familiarity with the underlying biology is of unquestionable value to all students of feed utilization, a more in-depth examination is beyond the scope of this review. All are encouraged to visit the excellent publication by Herd and Arthur (2009).

**Challenges and Opportunities of the Present and Future**

The greatest impediment to widespread improvement in feed utilization efficiency is the difficulty and expense of measuring individual feed intake. Modern systems such as Calan® Broadbent and GrowSafe® are vastly superior to earlier methods, such as individual housing or tying out animals for individual feeding sessions. However, while the most progressive seedstock producers are beginning to record individual intake data, it may still be many more years before the practice is as widely adopted as that of measuring growth traits (e.g., weaning weight). And, it is likely that intake data collection will always remain prohibitively expensive for commercial cow-calf operators. But until intake is more commonly measured—or, at least, among more of the animals making significant genetic contributions—substantial progress in efficiency will likely remain elusive. It is possible that markers will enhance our ability to estimate efficiency, and could be incorporated into breeding strategies (Sherman et al., 2010).

Genuine improvement in efficiency requires that more marketable product is generated from a specified amount of inputs. Rapid growth of calves of usually gives more attractive FCR values. But, this advantage must be weighed against the likelihood of bigger
cows that require a larger amount of pasture or supplemental feed. Additionally, carcass weights outside the currently acceptable range suffer price discounts; cattle that mature at a greater size are more likely to produce excessively heavy carcasses. Of course, one must also be careful not to pursue a measure of efficiency that leads to inadequate growth. It must also be kept in mind that longevity and reproductive capability are key components to overall efficiency. Additional research is needed to ensure that such traits are not negatively affected by apparent improvement in feed utilization. The path to more efficient beef production is not simple. Nevertheless, enormous rewards await those who pursue it.


CHAPTER 2

Relationships Among Feed Utilization and Performance Traits in Developing Angus Heifers
Introduction

Feed is the largest single variable cost in beef production (Arthur et al., 2001a). In 2009, total cash receipts from the sale of meat animals in the United States were $58.6 billion. Cattle and calves accounted for 75 percent of that total (NASS, USDA, Agricultural Statistics Board, 2010). Thus, improving efficiency of feed utilization by beef cattle would directly impact the food animal industry. However, the optimal approach for achieving genetic improvement is not yet as clear. There are several traits related to the efficiency of feed utilization, each having its own advantages and challenges. All require measurement of feed consumption—the major factor limiting their implementation by cattle breeders.

There is evidence of genetic variation and the potential of selection for improved efficiency (e.g., Archer et al., 1999). Gross efficiency (gain:feed) or its inverse, feed conversion ratio (FCR; feed:gain), has long served as a standard measure of feed efficiency. However, the strong correlation between gross efficiency and growth (Brelin and Brannang, 1982; Mrode et al., 1990) may be cause for concern. While increased growth rate is welcomed in the feedlot and harvest sectors, correlated response that increases mature cow size would elevate feed costs associated with maintenance of the breeding herd (Archer et al., 1999). Approximately 65% to 75% of overall energy costs for beef production go into the cow herd. Of that amount approximately 70% goes for maintenance energy (Ferrell and Jenkins, 1984). If adult stock are deemed not excessively large for their environment and purpose, and increased growth rate is sought, then gross efficiency would be an appropriate measure of efficiency. A separate disadvantage limiting the usefulness of gross efficiency or FCR is that no consideration is given to the animal’s body weight and the amount of feed
required for maintenance. Furthermore, additional problems plaguing ratio-based selection in general have been identified by Gunsett (1984). Such issues include a more unpredictable and less efficient response then if a linear index were to be used instead.

Partial efficiency of growth (PEG) is another measure of efficiency. It is the ratio of weight gain to the portion of consumed feed remaining after deduction of feed intake required for maintenance. A major advantage of PEG over FCR is its attempt to account for maintenance needs. However, the trait’s problems also stem from this effort. Estimation of maintenance requirements either necessitates metabolic trials, or relies upon standards published in resources such as the National Research Council’s *Nutrient Requirements of Beef Cattle* (NRC, 2000) or the Standing Committee on Agriculture’s *Feeding Standards for Australian Livestock* (SCA, 1990). The former approach is relatively difficult—especially in growing animals—and would not be practical in large studies. The latter method implies no variation in maintenance efficiency—an assumption not supported in the literature (Archer et al., 1999).

Residual feed intake (RFI), introduced by Koch et al. (1963), allows for feed efficiency selection that is phenotypically independent of growth rate. Residual feed intake is the difference between an animal’s actual intake and its expected intake after accounting for body weight and growth (other variables influencing intake could also be included). Prediction of intake can be made either by phenotypic regression within the dataset, or with standard equations utilizing feed nutrient values and animal requirements. Adjustment for body weight and growth rate in the intake prediction forces RFI and these traits to be phenotypically independent. (This seems to be more consistently reported for the regression
method, as standard equations rarely fit a population perfectly and phenotypic correlations with size or growth may exist.) However, genetic independence of RFI with weight or growth is not guaranteed (Kennedy et al., 1993), and further characterization of these relationships is needed. Additionally, Kennedy et al., (1993) and van der Werf (2004) have shown that including RFI in a selection index offers no advantage over an index containing the constituent traits.

Along with size and growth traits, ultrasonographic evaluations of carcass-related traits were also included in this study. Specifically, these included ultrasound ribeye (longissimus dorsi muscle) area, intramuscular fat percentage, and fat thickness at rib and rump sites. Other studies have generally suggested a weak to moderate, positive correlation of RFI with fat thickness, but no significant association with ribeye area or intramuscular fat (Arthur et al., 2001a; Baker et al., 2006; Basarab et al., 2003; Lancaster et al., 2009a; Nkrumah et al., 2004; Schenkel et al., 2004).

Additionally, the thyroid hormones 3,5,3’-triiodothyronine (T₃) and thyroxine (T₄) were included in this study. Their influential roles in metabolism (Lawrence and Fowler, 1997) prompted investigation of their potential utility as indicators of DMI or efficiency traits.

The benefits of understanding relationships of feed efficiency traits with other traits are at least two-fold: 1) discovery and subsequent utilization of indicator traits, and 2) improved awareness of correlated responses. Measuring feed intake has historically been an expensive, time- and labor-demanding venture. While technological advances such as the GrowSafe® System (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) have made intake
data collection much more convenient, the initial investment remains substantial. If a more easily measured trait were correlated strongly enough with intake (or efficiency itself), it could be used as a proxy for intake in feed efficiency evaluations. Additionally, a more thorough understanding of the relationships would allow construction of more effective selection indices.

The objective of this study was to examine relationships of feed utilization traits amongst each other and with performance traits, including growth, ultrasound estimates of body composition, and indicators of reproductive soundness.

**Materials and Methods**

The protocol for this project was reviewed and approved by the NCSU Institutional Animal Care and Use Committee (#08-089).

**Description of Animals**

Heifers (n = 208) utilized in this study were from the Angus herd maintained at Upper Piedmont Research Station (UPRS) near Reidsville, North Carolina. The calving season at UPRS extended from mid-November through January, with weaning occurring in June. Heifers were vaccinated against respiratory and clostridial diseases and dewormed. In total, 33 sires were represented by daughters in the study, and 4 of these also had granddaughters. Ninety-four dams were represented by 1 daughter each, while 40 dams had 2 daughters each, 10 dams had 3, and 1 dam had 4 daughters. Ages and weights on-test and
number of sires by year are presented in Table 1.

**Description of Trial**

**Housing and feeding system**

Heifers were blocked by body weight (BW) into 2 groups and placed in adjacent dry lots. Use of the Calan® Broadbent feeding system (American Calan, Northwood, NH) allowed individual feed intake to be measured. Heifers were allowed 14 d of acclimation to the ration and Calan® gates prior to the start of the official trial. Two heifers were observed eating from another heifer’s feeder during the trial and were immediately removed from the study.

**Diet ingredients and composition**

Feed rations were roughage-based and formulated for 0.91-kg ADG. Composition and analysis values can be found in Table 2. The Year 1 ration had a corn-silage base, while hay was the primary ingredient in the following 3 years.

**Data collection**

Following the 14-d pre-trial adjustment period, feed intake data were collected for 84 d. Fresh feed was delivered once daily with a Data Ranger® (American Calan, Northwood, NH). The amount was adjusted accordingly to provide as near to *ad libitum* access as possible while minimizing excessive accumulation of uneaten feed (orts). Orts were weighed and removed every 7 d, or sooner if wet or in excess. Average daily dry matter intake (DMI)
over the 84-d trial was calculated for each heifer from these data as the sum of weekly totals of (dry) feed offered minus (dry) orts.

At the beginning (Day 1 ± 7 d, middle (Day 42 ± 7 d), and conclusion (Day 84 ± 7 d) of each trial, heifers were ultrasonically scanned by a certified technician, hip height was recorded, and a blood sample, for thyroid hormone assays, was collected.

Beginning weight (BegWt) and final weight (EndWt) were the average of weights taken on Days 1 and 2 and Days 84 and 85, respectively. Heifers were also weighed every 14 d.

**Description of Traits**

**Efficiency and Performance**

Average daily gain (ADG) was calculated from the regression of BW on time (day of trial). Body weight at mid-point of trial (MidWt) was found by the equation,

\[
\text{MidWt} = \text{BegWt} + 42(\text{ADG}).
\]

This mid-trial weight was converted to a metabolic basis by raising this value to the 0.75 power (MetMW = MidWt\(^{0.75}\)).

Feed conversion ratio (FCR) was defined as DMI/ADG. Partial efficiency of growth (PEG) was computed as the ratio of ADG to DMI used for growth. This DMI available for growth was determined by first finding DMI required for maintenance (Lancaster et al., 2009a; NRC, 2000), with

\[
\text{DMI for maintenance} = \frac{[(0.077* \text{MetMW}) / \text{NE concentration in the ration}]}{
\]

That amount for maintenance was subsequently subtracted from total DMI.
Three different approaches were taken in predicting DMI for use in calculating RFI. The first method relied on prediction equations provided by NRC (2000). The amount of net energy for maintenance (NEm) required per unit of empty, shrunk, metabolic body weight was determined. Likewise, the amount of net energy for gain (NEg) required per unit of weight gain was also found. These requirements were applied, in conjunction with NEm and NEg content of the ration, to determine the amount of feed required by each heifer for her unique combination of growth rate and body weight maintained. Actual observed DMI minus this expected intake gave RFInrc. A similar technique was employed by Fan et al. (1995).

The second method predicted DMI on the basis of weight alone. The formula was derived from SCA (1990). Six hundred kilograms was chosen as an appropriate Standard Reference Weight (SRW) for this population, based on mature dam weights. The SRW is the expected weight after an animal has attained full skeletal size and is conditioned such that 25% of its empty-body weight is fat. Therefore,

$$\text{RFIsca} = \text{DMI} - [0.024 \times 600 \times \left(\frac{\text{MidWt}}{600}\right) \times (1.7 - (\frac{\text{MidWt}}{600}))].$$

The third approach modeled DMI by phenotypic regression on MetMW and ADG. Inclusion of ultrasound traits was also considered (Basarab et al., 2003; Lancaster et al., 2009a; Lancaster et al., 2009b; Schenkel et al., 2004). However, none of them reached significance ($P > 0.08$) in the model and contributions to the coefficient of determination ($R^2$) were small (0.001 - 0.044). The GLM Procedure of SAS (Version 9.1, SAS Inst., Inc. Cary, NC) was used in modeling intake. Coefficients of determination were 0.678, 0.741, 0.340, and 0.679 for Years 1, 2, 3, and 4, respectively. No explanation could be found for the
reduced fit in Year 3. Residual feed intake by this method is therefore defined as the residual error term of this intake model. That is,
\[ RFI_{\text{reg}} = DMI - [\beta_0 + \beta_1(\text{MetMW}) + \beta_2(\text{ADG})], \]
where DMI is observed dry matter intake, \( \beta_0 \) is the intercept term in the intake prediction model, and \( \beta_1 \) and \( \beta_2 \) are regression coefficients for MetMW and ADG, respectively.

**Ultrasound body composition**

Heifers were scanned with an Aloka 500® (Aloka Co., Wallingford, CT) by an Ultrasound Guidelines Council (UGC)-certified technician. Images were submitted to the Centralized Ultrasound Processing (CUP) Lab (Ames, IA), where lab analysis produced measures of ribeye area, percentage intramuscular fat of the ribeye, and fat thickness at the ribs and on the rump. Ribeye area and rib fat were assessed between the 12th and 13th ribs, and rump fat at the juncture of the \( m. \text{gluteus medius} \) and \( m. \text{biceps femoris} \). Heifers were scanned at the beginning, middle, and end of trial, as described previously. Data from the final (third) scan were also submitted to the American Angus Association. Additionally, for this study, ribeye area was scaled for animal size, resulting in REcwt (final uRE / (scan weight, kg / 45.4 kg).

**Behavior**

Behavioral traits of the heifers were also assessed. Exit velocity (EV) was measured by placing a motion sensor 1.83 m beyond the release point (front) of the squeeze chute and a second motion sensor 1.83 m beyond the first. The distance between sensors (1.83 m) was
then divided by the time required for a heifer to traverse that distance, giving EV in m/s.

Temperament score (TS; 1-5) was also recorded, based upon a heifer’s observed disposition just prior to her entering the squeeze section of the chute. Animals receiving TS of 1 were very calm, while animals scored TS of 5 appeared extremely agitated. Initially, EV and TS were evaluated at each of the three ultrasound events (start, middle, and end of trial). After Year 2, it became apparent that frequent handling of the heifers (bi-weekly weighing) was having a calming effect and reducing variation in EV and especially TS. Being accustomed to human contact and being moved through the chute system, most heifers behaved well and exited slowly. In an attempt to capture more of the variation among the animals, EV was recorded at weaning (approximately 2 months prior to beginning of trial) instead of during the trial, beginning in Year 3. During this time of transition, TS was inadvertently not recorded in Year 3. Both EV and TS were recorded at weaning in Year 4. For Years 1 and 2, EV and TS from only the first recorded event (beginning of trial) were included in the analysis.

Reproduction

In Year 4, an attempt was made to include reproductive traits, in order to assess the likelihood of correlated response in fertility due to selection on efficiency. This initial effort involved only reproductive tract score (RTS). Each heifer was rectally palpated and assigned an RTS based upon perceived maturity of the reproductive tract. Possible scores ranged from 1 to 5, with a lower score indicating a less mature tract. Guidelines for RTS assignment are presented in Table 3. Heifers were first scored 4 d after the conclusion of the formal trial.
(RTS1). Heifers were evaluated again 66 d after conclusion of the trial (RTS2).

**Endocrine**

Assays for free T₃ and free T₄ were conducted using radioimmunoassay kits from Diagnostic Products Corporation (DPC, Los Angeles, CA). Assays were conducted according to instructions supplied by manufacturer. The kits provided either ¹²⁵I-labeled T₃ or T₄, known amounts of T₃ or T₄ for standards, and tubes coated with antibodies to either T₃ or T₄. Briefly, the procedure for both assays was as follows. One hundred µl of either standard or serum from experimental animals was added to antibody-coated tubes. The standards ranged from 0 to 60 ng/ml. Then 1 ml of ¹²⁵I-labeled T₃ or T₄ was added to these tubes, as well as to four polypropylene tubes. Two of these tubes were counted in the gamma counter with the ¹²⁵I-labeled T₃ or T₄ still in the tubes to determine total counts. In the other two tubes, the liquid was decanted and the empty tubes were counted to determine non-specific binding. After a 2-hour incubation in a 37° C water bath, the tubes were decanted to remove the liquid, left upside down for approximately 15 minutes to dry, and then counted for 1 minute in a gamma counter and results compared to the standard curve by use of log-logit transformation (Rodbard and Lewald, 1970) to determine serum concentrations.

**Statistical Analyses**

**Phenotypic correlation**

The CORR Procedure of SAS (Version 9.1, SAS Inst., Inc. Cary, NC) was used to generate Pearson partial (adjusted for Year) phenotypic correlation coefficients. The focus of
this analysis was phenotypic associations of efficiency and component traits with other
efficiency, production, and behavioral traits.

*Heritability and genetic correlation*

Analysis of genetic parameters was conducted with MTDFREML, using an Animal
model. A 5-generation pedigree for the heifers was utilized. Heifers (n=4) whose sires (n=2)
had fewer than 3 progeny tested were excluded from genetic analysis. Year was included as
a fixed-effect variable for all traits. Age of dam (two levels: primi- or multiparous) was
added to the model for yearling hip height (YrHipHt). Convergence was assumed for an
iteration when variance of -2 times the log likelihood used in simplex search algorithm was
less than $10^{-10}$. To guard against local maxima, cold restarts using the previous convergence
values were performed until results did not change for three consecutive runs.

*RFI Groups*

Heifers were categorized by MTDFREML-estimated breeding values for RFIreg.
Heifers (n = 71) in the High Group had RFIreg breeding values more than 0.44 standard
deviations above the mean RFIreg breeding value for all heifers (i.e., High breeding value >
$[-0.0102 + 0.44*0.1608]$). Heifers (n = 69) in the Low Group had RFIreg breeding values
more than 0.44 standard deviations below the mean breeding value. Heifers (n = 64) of the
Medium Group had RFIreg breeding values within 0.44 standard deviations of the mean
RFIreg breeding value. It should be recognized that higher breeding values would indicate
lower efficiency (higher RFIreg).
The MIXED Procedure of SAS (Version 9.1, SAS Inst., Inc. Cary, NC) was used to estimate the effect of RFIreg Group on traits of interest. The base model included Year and RFIreg Group. In the DMI model, MidWt and ADG were added to the base model as covariates. The model for RTS included the addition of age and EndWt to the base model, while Year became unnecessary and was removed.

**Results and Discussion**

*Efficiency Traits*

Much of the variation among the years (Table 1) in efficiency traits is likely due to differences in ration composition and quality, while other environmental factors and genetic differences also contributed. Additionally, it is also worth noting that a more nutrient-dense diet supporting higher rates of gain likely would have allowed more expression of differences in performance and perhaps efficiency. However, the diet type in this study is similar to that provided for replacement heifers in many commercial beef operations.

Negative means for RFIsca in all years indicate that the equation overestimated DMI in this population—an outcome also reported by Hennessy and Arthur (2004) but not by Robinson and Oddy (2004). Overestimation of intake for RFInrc could be due to the prediction equations having been developed for a different diet type. All three types of RFI were positively phenotypically correlated with each other and with FCR (Table 4a). Partial efficiency of growth had a negative phenotypic correlation with all RFI traits and with FCR (as expected, since greater efficiency is signified by higher values for PEG but lower values
for the other traits). The phenotypic correlation between FCR and RFIreg (r = 0.31) is lower than most estimates found in published literature, which tend to range from 0.40 to 0.65 (see Chapter 1). Differences in FCR among RFIreg groups (Table 7) also support an association between FCR and RFIreg.

Heritability estimates for several traits are substantially higher than most published estimates. Among efficiency traits, heritability of RFIsca at 0.56 ± 0.167 is quite high, especially in comparison to a published estimate of 0.13 ± 0.05 (Robinson and Oddy, 2004). Heritabilities of other efficiency traits (Table 5) were in agreement with published estimates. While most were not statistically different from zero, all of the genetic correlations among RFI traits and FCR were positive, with the exception of RFIsca and FCR’s negative association. There was quite a range among Spearman rank correlations. Some efficiency traits showed similar rankings, most notably PEG, FCR, and RFInrc. Rankings on the basis of RFIreg would agree least with rankings by other efficiency traits.

Intake, Gain, and Size

All efficiency traits were phenotypically and genetically correlated with DMI, in the direction of less efficient animals exhibiting greater intake (with the exception of RFInrc, which showed a negative (non-significant) genetic correlation). While the phenotypic correlation of 0.43 between RFIreg and DMI was slightly lower than is usually reported (most estimates fall between 0.60 and 0.75—see Chapter 1), their genetic relationship agreed very well with estimates reported in the literature. Significant differences in DMI among RFIreg breeding value groups further corroborated the idea that higher-RFIreg animals
consume more feed.

Phenotypic correlation of virtually zero between RFIreg and ADG was expected. Among other efficiency traits, phenotypic correlations indicated higher rate of gain for more efficient animals in all but RFIsca. The strong, negative correlations between FCR and ADG are supported in the literature. The genetic correlation with ADG is negative for RFInrc, yet positive for RFIsca. The positive genetic correlation (0.43 ± 0.313) of RFIreg with ADG would be unfavorable for breeders seeking both rapid gain and efficiency (as measured by RFIreg). Elzo et al. (2009) also reported a positive genetic correlation between RFIreg and post-weaning gain (0.58 ± 0.28) in their population of Angus, Brahman, and hybrid calves (n = 581). Also, Hoque et al. (2006) observed a positive genetic correlation (0.25 ± 0.16) in Wagyu bulls (n = 740). However, most cattle RFI studies that have included genetic analysis have reported RFIreg to be genetically independent of ADG (Arthur et al., 2001a; Arthur et al., 2001b; Crowley et al., 2010; Herd and Bishop, 2000; Jensen et al., 1992; Lancaster et al., 2009b; Schenkel et al., 2004). Still, further investigation of the true genetic relationship between RFIreg and ADG appears to be warranted.

Phenotypic relationships with MidWt and HipHt suggest that efficiency traits generally tend to favor smaller animals, with RFInrc and—especially—RFIreg being the exceptions (neutral). Genetic relationships among efficiency and size traits are somewhat mixed. (Convergence criteria in genetic analysis could not be satisfactorily met for measures of weaning weight, yearling weight, and yearling hip height adjusted by American Angus Association.)
Ultrasound Traits

Phenotypic correlations of efficiency traits with ultrasound measurements tended to mirror their relationships with size. For instance, positive correlation of FCR both with RpFT and with REA is probably more attributable to their mutual association with MidWt than to any special connection between efficiency and carcass-related characteristics. Similarly, relationships with gains in ultrasound traits appeared to be linked to relationships with ADG. Additionally, correlations with REAcwt generally tended to be similar to those of ribeye area without adjustment for weight, as BW and ribeye area are strongly associated. Differences were not observed for ultrasound traits among RFIreg groups.

Other Traits of Interest

Results for behavioral traits were somewhat difficult to interpret. Phenotypic correlations with EV indicate that heifers exiting more slowly showed higher DMI and were less efficient by PEG, RFInrc, RFIsca. Phenotypic correlations with TS suggest that more excitable heifers had greater DMI and were less efficient—by every measure but RFIreg (nearly neutral). Animals assigned higher TS were heavier, but those with quicker exit speeds were lighter. Heritabilities for EV and TS were not statistically different from zero. Both traits appeared unfavorably genetically correlated with FCR (higher FCR for calmer heifers). For the three RFI traits, genetic correlations were positive (favorable) for EV but negative (unfavorable) for TS. No significant differences in behavioral traits were observed among RFIreg groups.

The thyroid hormone T₃ is at least somewhat promising as an indicator of feed
utilization efficiency. Every efficiency trait except RFI\textsubscript{reg} was phenotypically correlated with T\textsubscript{3} (in the direction of more efficient animals having higher free T\textsubscript{3} concentrations). Free T\textsubscript{3} was negatively correlated with DMI and positively correlated with ADG; this helps explain its association with efficiency traits. But, its relationship with DMI could be due to its correlation with MidWt. It may be that light yet fast-growing calves have the highest free T\textsubscript{3} concentrations. Lack of correlation between free T\textsubscript{3} and RFI\textsubscript{reg} would seem to support the notion that concentration of the hormone is tied to size and growth rate, but perhaps not to inherent metabolic efficiency per se.

No significant differences in Milk EPD were observed among RFI\textsubscript{reg} groups. Given the relationship between milk production potential and maintenance efficiency (see Chapter 1), there may, in fact, be a connection. However, this was not an ideal method for testing that hypothesis.

In the one year that RTS was evaluated, there was a favorable trend for heifers in more efficient groups (lower RFI\textsubscript{reg} breeding values) to have higher RTS. This held true for both RTS evaluations. At the first scoring, the Low-RFI Group tended (P = 0.06) to have higher RTS\textsubscript{1} than the High Group, with the Medium Group intermediate. This trend grew more apparent by the second evaluation, with Low heifers having significantly greater (P = 0.02) RTS\textsubscript{2} than High Group heifers. Medium heifers were again intermediate, but their trend in difference (P = 0.10) from the High Group strengthened. However, this is far from conclusive evidence of a relationship between reproductive capability and RFI. One must bear in mind the small numbers involved in this study. Still, it may be that larger trials would support this conclusion. Reproductive efficiency is critically important to overall efficiency...
(and profitability) of beef production. Further investigation of the relationship between reproductive ability and RFI is necessary. In any future studies similar to this one, accurately measuring age at puberty would be worthy of consideration. Perhaps heifers involved in this study will someday play a role in a dam productivity investigation.

In conclusion, additional work remains to be done in the field of feed efficiency in cattle. Exploration of relationships between measures of efficiency and other traits must continue, especially while the underlying physiology remains so nebulous. It would seem that something with an energetic cost must be sacrificed for an animal to “eat less than expected.” Savings in feed costs may not be worth impairment of immune or reproductive systems. Efficiency will become even more important if the beef industry wishes to remain viable on a planet where natural resources seem stretched increasingly thin. An ideal solution would be beneficial to both the cow-calf and the feedlot sectors. A perfectly weighted economic selection index would be the key.
Literature Cited


Table 1. Animal numbers and trait means with standard errors by year.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Yr1 Mean</th>
<th>Yr1 SEM</th>
<th>Yr2 Mean</th>
<th>Yr2 SEM</th>
<th>Yr3 Mean</th>
<th>Yr3 SEM</th>
<th>Yr4 Mean</th>
<th>Yr4 SEM</th>
<th>Overall Mean</th>
<th>Overall SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beginning age (days)</td>
<td>299±3.2</td>
<td>286±2.8</td>
<td>256±2.6</td>
<td>284±2.5</td>
<td>273±1.9</td>
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<tr>
<td>BegWt (kg)</td>
<td>270±4.9</td>
<td>290±4.8</td>
<td>250±3.2</td>
<td>242±4.5</td>
<td>263±2.5</td>
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<tr>
<td>MidWt (kg)</td>
<td>314±4.6</td>
<td>327±4.4</td>
<td>288±4.5</td>
<td>287±4.3</td>
<td>299±2.8</td>
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<tr>
<td>EndWt (kg)</td>
<td>362±5.0</td>
<td>363±4.7</td>
<td>328±4.8</td>
<td>298±4.8</td>
<td>337±3.0</td>
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<tr>
<td>DMI (kg/d)</td>
<td>5.44±0.099</td>
<td>7.76±0.110</td>
<td>6.61±0.097</td>
<td>6.50±0.101</td>
<td>6.61±0.077</td>
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<td>ADG (kg)</td>
<td>1.04±0.029</td>
<td>0.88±0.019</td>
<td>0.89±0.019</td>
<td>0.61±0.016</td>
<td>0.85±0.015</td>
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<tr>
<td>FCR</td>
<td>5.37±1.07</td>
<td>8.96±1.74</td>
<td>7.57±1.46</td>
<td>11.07±3.02</td>
<td>8.30±1.74</td>
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<tr>
<td>PEG</td>
<td>0.68±0.027</td>
<td>0.23±0.004</td>
<td>0.30±0.010</td>
<td>0.20±0.005</td>
<td>0.35±0.015</td>
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<td>PFin  (kg)</td>
<td>-3.59±0.158</td>
<td>-6.62±0.080</td>
<td>-1.06±0.010</td>
<td>0.54±0.067</td>
<td>-1.13±0.116</td>
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<td>RFisca (kg)</td>
<td>-3.37±0.083</td>
<td>-1.23±0.074</td>
<td>-1.80±0.101</td>
<td>-1.51±0.071</td>
<td>-1.95±0.070</td>
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<td>RFIing (kg)</td>
<td>0±0.056</td>
<td>0±0.056</td>
<td>0±0.079</td>
<td>0±0.057</td>
<td>0±0.031</td>
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<td>HipHt (cm)</td>
<td>119.4±0.69</td>
<td>120.1±0.53</td>
<td>114.6±0.58</td>
<td>115.3±0.56</td>
<td>117.3±0.33</td>
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<tr>
<td>AdjRFtRt (cm²)</td>
<td>8.36±0.235</td>
<td>9.76±0.226</td>
<td>7.23±0.230</td>
<td>5.08±0.226</td>
<td>7.59±0.166</td>
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<td>AdjRFtL (cm²)</td>
<td>5.92±0.173</td>
<td>6.91±0.166</td>
<td>5.40±0.168</td>
<td>3.01±0.166</td>
<td>5.30±0.131</td>
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<tr>
<td>AdjIMF (%)</td>
<td>5.70±0.116</td>
<td>5.92±0.128</td>
<td>6.07±0.136</td>
<td>5.76±0.122</td>
<td>5.86±0.064</td>
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<tr>
<td>AdjREA (cm²)</td>
<td>54.3±0.94</td>
<td>64.3±0.90</td>
<td>57.6±0.91</td>
<td>52.7±0.90</td>
<td>57.3±0.55</td>
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<tr>
<td>REAcwt (cm²)</td>
<td>6.93±0.098</td>
<td>7.68±0.180</td>
<td>7.40±0.096</td>
<td>7.23±0.084</td>
<td>7.32±0.051</td>
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<tr>
<td>T3beg (gg/ml)</td>
<td>2.04±0.114</td>
<td>1.61±0.048</td>
<td>3.75±0.112</td>
<td>1.31±0.076</td>
<td>2.17±0.080</td>
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<tr>
<td>T3mid (gg/ml)</td>
<td>3.70±0.185</td>
<td>1.87±0.040</td>
<td>3.09±0.112</td>
<td>1.85±0.101</td>
<td>2.60±0.080</td>
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<tr>
<td>T3end (gg/ml)</td>
<td>3.33±0.165</td>
<td>1.59±0.060</td>
<td>3.42±0.136</td>
<td>2.10±0.114</td>
<td>2.58±0.081</td>
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<tr>
<td>T4beg (ng/dl)</td>
<td>0.395±0.0136</td>
<td>0.501±0.0128</td>
<td>0.839±0.0271</td>
<td>0.763±0.0205</td>
<td>0.653±0.0152</td>
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<tr>
<td>T4mid (ng/dl)</td>
<td>0.701±0.0162</td>
<td>0.562±0.0219</td>
<td>0.756±0.0296</td>
<td>0.562±0.0143</td>
<td>0.671±0.0120</td>
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<tr>
<td>T4end (ng/dl)</td>
<td>0.518±0.0123</td>
<td>0.524±0.0193</td>
<td>0.729±0.0339</td>
<td>0.626±0.0144</td>
<td>0.625±0.0119</td>
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<tr>
<td>EV (ml/s)</td>
<td>2.42±0.166</td>
<td>1.82±0.090</td>
<td>2.06±0.151</td>
<td>3.56±0.195</td>
<td>2.46±0.089</td>
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<tr>
<td>TS (1-5)</td>
<td>1.29±0.077</td>
<td>2.85±0.199</td>
<td>1.45±0.079</td>
<td>1.88±0.079</td>
<td></td>
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</tr>
</tbody>
</table>

1. Multi-year sites counted only once.
2. Within a row, Year mean values without common superscripts differ (P < 0.05).
3. Begw = initial weight at start of trial.
4. Midw = mid-trial weight = beginning weight + 42/ADG.
5. Endw = actual weight at end of trial.
6. AdjFin = Residual feed intake for which predicted feed intake was calculated with prediction equations from NRC (2000).
7. AdjFisca = Residual feed intake for which predicted feed intake was calculated with a prediction equation from SCA (1990).
8. AdjPre = Residual feed intake for which predicted feed intake was calculated with a multivariate linear model adjusting for ADG and mid-trial metabolic BW.
9. HipHt = Unadjusted hip height recorded at the third ultrasound date (end of trial).
11. REAcwt = real ultrasound ribeye area / (BW at scan / 45.4kg).
12. Free T3: Blood for assays collected at first (beg), second (mid), and final (end) ultrasound dates.
13. Free T4: Blood for assays collected at first (beg), second (mid), and final (end) ultrasound dates.
15. TS = Temperament score. Recorded at first ultrasound in Years 1 and 2 and at weaning in Year 4. Not recorded in Year 3.
Table 2. Ration composition and values.

<table>
<thead>
<tr>
<th>TMR Ingredients¹</th>
<th>Mean analysis values (DM basis):</th>
</tr>
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<tbody>
<tr>
<td>Fescue hay:</td>
<td>48% TDN: 61.1%</td>
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<tr>
<td>Soy hulls:</td>
<td>25% NEm: 1.34 Mcal/kg</td>
</tr>
<tr>
<td>Corn gluten feed</td>
<td>25% NEg: 0.77 Mcal/kg</td>
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<tr>
<td>Mineral mix:</td>
<td>1.5% CP: 13.7%</td>
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<tr>
<td>Limestone:</td>
<td>0.5% Ca: 0.73%</td>
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</table>

¹For Years 2-4

Table 3. Reproductive Tract Score criteria.

<table>
<thead>
<tr>
<th>RTS</th>
<th>Uterine Horns</th>
<th>Ovarian Dimensions (mm)</th>
<th>Ovarian Structures</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Diameter</td>
<td>Tone</td>
<td>Length</td>
</tr>
<tr>
<td>1</td>
<td>&lt; 20mm</td>
<td>No tone</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>20-25mm</td>
<td>No tone</td>
<td>18</td>
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<tr>
<td>3</td>
<td>25-30mm</td>
<td>Slight</td>
<td>22</td>
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<tr>
<td>4</td>
<td>30mm</td>
<td>Good</td>
<td>30</td>
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</tr>
<tr>
<td>5</td>
<td>&gt; 30mm</td>
<td>Excellent</td>
<td>32</td>
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Adapted from Anderson et al., 1991.
<table>
<thead>
<tr>
<th></th>
<th>PEG</th>
<th>RFInrc&lt;sup&gt;1&lt;/sup&gt;</th>
<th>RFIsca&lt;sup&gt;2&lt;/sup&gt;</th>
<th>RFIreg&lt;sup&gt;3&lt;/sup&gt;</th>
<th>DMI</th>
<th>ADG</th>
<th>MidWt&lt;sup&gt;4&lt;/sup&gt;</th>
<th>HipHt&lt;sup&gt;5&lt;/sup&gt;</th>
<th>T3beg&lt;sup&gt;6&lt;/sup&gt;</th>
<th>T3mid&lt;sup&gt;7&lt;/sup&gt;</th>
<th>T3end&lt;sup&gt;7&lt;/sup&gt;</th>
<th>T4beg&lt;sup&gt;7&lt;/sup&gt;</th>
<th>T4mid&lt;sup&gt;7&lt;/sup&gt;</th>
<th>T4end&lt;sup&gt;7&lt;/sup&gt;</th>
<th>EV&lt;sup&gt;8&lt;/sup&gt;</th>
<th>TS&lt;sup&gt;9&lt;/sup&gt;</th>
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</thead>
<tbody>
<tr>
<td>FCR</td>
<td>-0.50**</td>
<td>0.70**</td>
<td>0.25**</td>
<td>0.31**</td>
<td>0.36**</td>
<td>-0.67**</td>
<td>0.32**</td>
<td>0.15*</td>
<td>-0.44**</td>
<td>-0.38**</td>
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<td>-0.13</td>
<td>-0.22**</td>
<td>-0.14*</td>
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<tr>
<td>PEG</td>
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<td>-0.42**</td>
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<td>-0.1</td>
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<td>-0.1</td>
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<tr>
<td>RFInrc&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0.61**</td>
<td>0.43**</td>
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<td>-0.36**</td>
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<tr>
<td>RFIsca&lt;sup&gt;2&lt;/sup&gt;</td>
<td>0.53**</td>
<td>0.86**</td>
<td>0.26**</td>
<td>0.13</td>
<td>0.18**</td>
<td>-0.06</td>
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<td>-0.38**</td>
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<tr>
<td>RFIreg&lt;sup&gt;3&lt;/sup&gt;</td>
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<tr>
<td>DMI</td>
<td>0.29**</td>
<td>0.62**</td>
<td>0.44**</td>
<td>-0.06</td>
<td>-0.37**</td>
<td>-0.39**</td>
<td>0.17*</td>
<td>-0.02</td>
<td>0.14*</td>
<td>-0.22**</td>
<td>0.53**</td>
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<tr>
<td>ADG</td>
<td>0.14*</td>
<td>0.20**</td>
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<td>0.16**</td>
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<td>MidWt&lt;sup&gt;4&lt;/sup&gt;</td>
<td>0.60**</td>
<td>-0.04</td>
<td>-0.23**</td>
<td>-0.18**</td>
<td>0.11</td>
<td>-0.09</td>
<td>0.07</td>
<td>-0.16*</td>
<td>0.19*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Different from zero (P ≤ 0.05).
** Different from zero (P ≤ 0.01).
<sup>1</sup>RFInrc = residual feed intake for which predicted feed intake was calculated with prediction equations from NRC (2000).
<sup>2</sup>RFIsca = residual feed intake for which predicted feed intake was calculated with a prediction equation from SCA (1990).
<sup>3</sup>RFIreg = residual feed intake for which predicted feed intake was calculated with a multivariate linear model adjusting for ADG and mid-trial metabolic BW.
<sup>4</sup>MidWt = mid-trial weight = beginning weight + 42(ADG).
<sup>5</sup>HipHt = actual hip height at third ultrasound date (end of trial).
<sup>6</sup>T3 = free T3 (pg/ml) at first ("beg"), second ("mid"), and final ("end") ultrasound dates.
<sup>7</sup>T4 = free T4 (ng/dl) at first ("beg"), second ("mid"), and final ("end") ultrasound dates.
<sup>8</sup>EV = exit velocity (m/s).
<sup>9</sup>TS = temperament score (1-5).
Table 4b. Partial phenotypic correlation coefficients, adjusted for year.

<table>
<thead>
<tr>
<th></th>
<th>RpFt⁵</th>
<th>RbFt⁶</th>
<th>IMF⁷</th>
<th>REA⁸</th>
<th>REAcwt⁹</th>
<th>GainRpFt¹⁰</th>
<th>GainRbFt¹¹</th>
<th>GainIMF¹²</th>
<th>GainREA¹³</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCR</td>
<td>0.21**</td>
<td>0.01</td>
<td>-0.06</td>
<td>0.27**</td>
<td>0.22**</td>
<td>-0.36**</td>
<td>-0.30**</td>
<td>-0.23**</td>
<td>-0.17**</td>
</tr>
<tr>
<td>PEG</td>
<td>-0.35**</td>
<td>-0.27**</td>
<td>0.00</td>
<td>-0.35**</td>
<td>-0.35**</td>
<td>0.04</td>
<td>0.01</td>
<td>0.15*</td>
<td>-0.15*</td>
</tr>
<tr>
<td>RFInrc¹</td>
<td>0.15*</td>
<td>0.00</td>
<td>-0.07</td>
<td>0.1</td>
<td>0.37**</td>
<td>-0.29**</td>
<td>-0.24**</td>
<td>-0.23**</td>
<td>-0.10</td>
</tr>
<tr>
<td>RFIsca²</td>
<td>0.29**</td>
<td>0.22**</td>
<td>0.01</td>
<td>0.21**</td>
<td>0.23**</td>
<td>-0.01</td>
<td>0.00</td>
<td>-0.13</td>
<td>0.09</td>
</tr>
<tr>
<td>RFIreg³</td>
<td>0.11</td>
<td>0.04</td>
<td>-0.01</td>
<td>0.09</td>
<td>0.09</td>
<td>0.13</td>
<td>0.02</td>
<td>-0.07</td>
<td>0.11</td>
</tr>
<tr>
<td>DMI</td>
<td>0.46**</td>
<td>0.42**</td>
<td>0.04</td>
<td>0.54**</td>
<td>0.18**</td>
<td>0.02</td>
<td>0.07</td>
<td>-0.15*</td>
<td>0.19**</td>
</tr>
<tr>
<td>ADG</td>
<td>0.08</td>
<td>0.23**</td>
<td>0.11</td>
<td>0.09</td>
<td>-0.20**</td>
<td>0.37**</td>
<td>0.33**</td>
<td>0.17*</td>
<td>0.27**</td>
</tr>
<tr>
<td>MidWt⁴</td>
<td>0.45</td>
<td>0.48**</td>
<td>0.06</td>
<td>0.70**</td>
<td>0.00</td>
<td>0.03</td>
<td>0.13</td>
<td>-0.09</td>
<td>0.20**</td>
</tr>
</tbody>
</table>

* Different from zero (P ≤ 0.05).
** Different from zero (P ≤ 0.01).
¹RFInrc = residual feed intake for which predicted feed intake was calculated with prediction equations from NRC (2000).
²RFIsca = residual feed intake for which predicted feed intake was calculated with a prediction equation from SCA (1990).
³RFIreg = residual feed intake for which predicted feed intake was calculated with a multivariate linear model adjusting for ADG and mid-trial metabolic BW.
⁴MidWt = mid-trial weight = beginning weight + 42(ADG).
⁵RpFt = actual ultrasound rump fat thickness measured at third ultrasound date.
⁶RbFt = actual ultrasound rib fat thickness measured at third ultrasound date.
⁷IMF = actual intramuscular fat percentage measured at third ultrasound date.
⁸REA = actual ribeye area measured at third ultrasound date.
⁹REAcwt = REA / (BW at scan / 45.4kg).
¹⁰GainRpFt = daily gain in ultrasound rump fat during trial; coefficient from regression of the three ultrasound rump fat measures on day of trial.
¹¹GainRbFt = daily gain in ultrasound rib fat during trial; coefficient from regression of the three ultrasound rib fat measures on day of trial.
¹²GainIMF = daily gain in ultrasound intramuscular fat percentage during trial; coefficient from regression of the three ultrasound intramuscular fat percentage measures on day of trial.
¹³GainREA = daily gain in ultrasound ribeye area during trial; coefficient from regression of the three ultrasound ribeye area measures on day of trial.
Table 5. Relationships among efficiency traits. Genetic correlations (with standard error) above diagonal, Spearman rank correlation coefficients\(^1\) below diagonal, and heritabilities\(^2\) on diagonal.

<table>
<thead>
<tr>
<th></th>
<th>FCR</th>
<th>RFInrc</th>
<th>RFIsca</th>
<th>RFIreg</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCR(^3)</td>
<td>0.24 (± 0.168); 0.22 - 0.27</td>
<td>0.37 (± 0.373)</td>
<td>-0.28 (± 0.343)</td>
<td>0.26 (± 0.393)</td>
</tr>
<tr>
<td>RFInrc(^4)</td>
<td>0.02</td>
<td>0.27 (± 0.160); 0.26 - 0.28</td>
<td>0.68 (± 0.240)</td>
<td>0.66 (± 0.203)</td>
</tr>
<tr>
<td>RFIsca(^5)</td>
<td>0.55</td>
<td>0.65</td>
<td>0.56 (± 0.187); 0.55 - 0.57</td>
<td>0.83 (± 0.116)</td>
</tr>
<tr>
<td>RFIreg(^6)</td>
<td>0.23</td>
<td>0.31</td>
<td>0.44</td>
<td>0.32 (± 0.158); 0.31 - 0.37</td>
</tr>
<tr>
<td>PEG(^7)</td>
<td>-0.95</td>
<td>-0.93</td>
<td>-0.73</td>
<td>-0.37</td>
</tr>
</tbody>
</table>

\(^1\)All Spearman rank correlation coefficients here are different from zero (\(P < 0.001\)).

\(^2\)Genetic analysis with MTDFREML. Heritability and standard error from single-trait analysis; range of heritabilities from two-trait analyses.

\(^3\)FCR = Feed conversion ratio (intake/gain).

\(^4\)RFInrc = Residual feed intake for which predicted feed intake was calculated with prediction equations from NRC (2000).

\(^5\)RFIsca = Residual feed intake for which predicted feed intake was calculated with a prediction equation from SCA (1990).

\(^6\)RFIreg = Residual feed intake for which predicted feed intake was calculated with a multivariate linear model adjusting for ADG and mid-trial metabolic BW.

\(^7\)PEG = Partial efficiency of growth. Genetic analysis unavailable.
<table>
<thead>
<tr>
<th></th>
<th>DMI</th>
<th>ADG</th>
<th>MidWt</th>
<th>YHRipFr</th>
<th>AdjRoFr</th>
<th>AdjRoFr</th>
<th>AdjIMF</th>
<th>AdjREA</th>
<th>REApm</th>
<th>EV</th>
<th>TS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hentability</td>
<td>0.72 ± 0.164</td>
<td>0.41 ± 0.168</td>
<td>0.76 ± 0.150</td>
<td>0.67 ± 0.154</td>
<td>0.30 ± 0.190</td>
<td>0.51 ± 0.174</td>
<td>0.36 ± 0.166</td>
<td>0.47 ± 0.173</td>
<td>0.08 ± 0.157</td>
<td>0.29 ± 0.230</td>
<td></td>
</tr>
<tr>
<td>FCR</td>
<td>0.19 ± 0.332</td>
<td>-0.41 ± 0.311</td>
<td>0.45 ± 0.272</td>
<td>0.04</td>
<td>-0.18</td>
<td>-0.24</td>
<td>0.40</td>
<td>0.39</td>
<td>-0.78</td>
<td>-0.93</td>
<td></td>
</tr>
<tr>
<td>RFIanc</td>
<td>-0.34 ± 0.283</td>
<td>-0.64 ± 0.233</td>
<td>-0.63 ± 0.213</td>
<td>-0.54</td>
<td>-0.20</td>
<td>-0.69</td>
<td>0.03</td>
<td>-0.46</td>
<td>0.33</td>
<td>0.35</td>
<td>-0.23</td>
</tr>
<tr>
<td>RFIasc</td>
<td>0.60 ± 0.143</td>
<td>0.60 ± 0.100</td>
<td>0.35 ± 0.276</td>
<td>-0.02</td>
<td>0.40</td>
<td>0.17</td>
<td>0.40</td>
<td>-0.22</td>
<td>-0.33</td>
<td>0.43</td>
<td>-0.47</td>
</tr>
<tr>
<td>RFIreg</td>
<td>0.72 ± 0.144</td>
<td>0.45 ± 0.313</td>
<td>0.17 ± 0.267</td>
<td>0.09</td>
<td>0.46</td>
<td>0.13</td>
<td>0.19</td>
<td>0.09</td>
<td>-0.14</td>
<td>0.50</td>
<td>-0.30</td>
</tr>
</tbody>
</table>

1 Heritability and standard error from MTDFREML single-trait analysis, with Year as a fixed effect (and Age of Dam for YHRipFr).
2 Genetic correlation and standard error (when available) from MTDFREML, with Year as a fixed effect (and Age of Dam for YHRipFr).
3 FCR = Feed conversion rate.
4 RFIanc = Residual feed intake for which predicted feed intake was calculated with prediction equations from NRC (2000).
5 RFIasc = Residual feed intake for which predicted feed intake was calculated with a prediction equation from SCA (1998).
6 RFIreg = Residual feed intake for which predicted feed intake was calculated with a multivariate linear model adjusting for ADG and mid-trial metabolic BW.
7 MidWt = mid-trial weight = beginning weight + 42/ADG.
8 YHRipFr = Hip height adjusted to 365 days of age (not by American Angus Association). Model for genetic analysis included fixed effect of Age of Dam (primi- or multiparous). In addition to Year.
10 AdjREA = Ribeye score.
11 REApm = final ultrasound ribeye area / (BW at scan 1 + 45.4 kg).
12 EV = exit velocity (m/s).
13 TS = temperament score (1-5). Not measured in Year 3.
<table>
<thead>
<tr>
<th>Trait</th>
<th>High</th>
<th>Medium</th>
<th>Low</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMI (kg/d)</td>
<td>7.02 ± 0.042</td>
<td>6.49 ± 0.044</td>
<td>6.16 ± 0.044</td>
</tr>
<tr>
<td>ADG (kg)</td>
<td>0.862 ± 0.0177</td>
<td>0.825 ± 0.0186</td>
<td>0.870 ± 0.0185</td>
</tr>
<tr>
<td>FCR</td>
<td>8.82 ± 0.161</td>
<td>8.18 ± 0.170</td>
<td>7.70 ± 0.169</td>
</tr>
<tr>
<td>AdjWnWt (kg)</td>
<td>229.5 ± 2.70</td>
<td>226.8 ± 2.83</td>
<td>233.7 ± 2.81</td>
</tr>
<tr>
<td>AdjYrWt (kg)</td>
<td>356.7 ± 3.53</td>
<td>343.1 ± 3.71</td>
<td>354.8 ± 3.66</td>
</tr>
<tr>
<td>AdjYrHt (cm)</td>
<td>117.7 ± 0.58</td>
<td>117.4 ± 0.56</td>
<td>118.7 ± 0.54</td>
</tr>
<tr>
<td>AdjRpFt (mm)</td>
<td>7.70 ± 0.197</td>
<td>7.50 ± 0.205</td>
<td>7.61 ± 0.2030</td>
</tr>
<tr>
<td>AdjRbf (in.)</td>
<td>5.35 ± 0.144</td>
<td>5.27 ± 0.151</td>
<td>5.32 ± 0.150</td>
</tr>
<tr>
<td>AdjIMF (%)</td>
<td>5.86 ± 0.109</td>
<td>5.82 ± 0.113</td>
<td>5.90 ± 0.112</td>
</tr>
<tr>
<td>AdjREA (cm²)</td>
<td>57.4 ± 0.78</td>
<td>56.4 ± 0.82</td>
<td>57.8 ± 0.81</td>
</tr>
<tr>
<td>REAwt (cm²)</td>
<td>7.26 ± 0.081</td>
<td>7.38 ± 0.086</td>
<td>7.30 ± 0.085</td>
</tr>
<tr>
<td>EV (m/s)</td>
<td>2.64 ± 0.127</td>
<td>2.43 ± 0.137</td>
<td>2.30 ± 0.133</td>
</tr>
<tr>
<td>TS (1-5)</td>
<td>1.82 ± 0.096</td>
<td>1.96 ± 0.097</td>
<td>1.81 ± 0.094</td>
</tr>
<tr>
<td>MilkEPD</td>
<td>20.59 ± 0.599</td>
<td>20.62 ± 0.629</td>
<td>21.46 ± 0.625</td>
</tr>
<tr>
<td>RTS1 (1-5)</td>
<td>1.37 ± 0.205</td>
<td>2.29 ± 0.227</td>
<td>2.35 ± 0.143</td>
</tr>
<tr>
<td>RTS2 (1-5)</td>
<td>2.03 ± 0.196</td>
<td>2.62 ± 0.216</td>
<td>2.60 ± 0.141</td>
</tr>
</tbody>
</table>

* Values in the same row with different superscripts differ (P < 0.001).
* Values in the same row with different superscripts differ (P < 0.005).
* Values in the same row with different superscripts differ (P < 0.05).
* Trait model includes Year, RFireg Group, and residual error term, unless otherwise specified.
* DMI model adds covariates ADG and Mid-test BW to the base model.
* AdjWnWt = 205-day Weaning Weight adjusted by American Angus Association.
* AdjYrWt = Yearling Weight adjusted by American Angus Association.
* AdjYrHt = Yearling Hip Height adjusted by American Angus Association.
* REAwt = final ultrasound ribeye area / (BW at scan / 45.4kg).
* EV = Exit velocity.
* TS = Temperament score.
* RTS = Reproductive Tract Score. Year 4 only. Model includes age, final weight, and RFireg Group. RTS1 evaluated 4 days after trial. RTS2 evaluated 66 days after trial.