Selection for Marbling and the Impact on Maternal Traits

Understanding the implications of selection for marbling in a cowherd

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Executive Summary

Although recent selection efforts within both the purebred and commercial beef sectors have focused on enhancing the genetic propensity for marbling within a cowherd, reports summarizing the presence or absence of relationships between marbling and maternal traits are limited. Concern currently exists related to the implications that these selection decisions may have on maternal traits within a cowherd. In order to address these concerns, a comprehensive literature review was conducted that summarizes and interprets results of research that has evaluated genetic and phenotypic relationships between marbling and traits related to maternal productivity. As part of the review, the most recent (Fall 2013) Angus Sire Evaluation Report was analyzed to determine the presence of potential relationships among relevant EPDs and dollar value ($Value) indices for Angus sires. An extensive review of the existing literature revealed that selection for improvements in marbling should not negatively impact scrotal circumference, age at puberty, heifer pregnancy, calving interval, or mature weight. Interestingly, there appears to be favorable relationships between marbling and birth weight, calving ease and the $W index. Additionally, relationships between marbling and milk yield, the $EN index, and mature height exist. Although interpretation of research conducted outside of the U.S. suggests a genetic link between these traits, little is known about the presence or absence of such relationships within U.S. cattle populations. The potential impact of the phenotypic relationships observed in the U.S. Angus sire population, however, will remain dependent upon management scenario and feed resources. As such, breeders are encouraged to remain cognizant of these relationships when making selection decisions, and as always, practice multiple trait selection while divergently selecting for these traits in such a way that matches progeny to a respective management strategy.

Introduction

One of the major factors that has led to a shift in the U.S. beef industry from its roots as a commodity-based market to its current state as a quality-based, value-added market has been the ability of cattlemen to identify and select for animals of superior carcass merit. This shift has provided the industry with the ability to ensure a remarkable degree of reliability in product quality and the consumer satisfaction that ensues. Following the turn of the century, the push for improvements in USDA carcass quality grade and overall consumer acceptance led to a strong desire amongst cattlemen throughout the country to place at least some degree of emphasis on selection for marbling development. As a result, a large number of producers have selected for cowherds that consist of females that possess an abundance of marbling potential.

At the 13th Annual Range Beef Cow Symposium held in Cheyenne, WY (1993), Field warned that selection for carcass traits may have implications to maternal productivity. A combination of the recent drought and high harvested feed costs across much of the United States has brought newfound light to the topic and left producers, 20 years later, asking the same question that Field began to address: has intensive selection for marbling and quality grade affected cowherd productivity?

Research efforts over the past two decades have primarily focused on indirectly evaluating the implications of intensive selection for marbling on maternal traits. As such, the objective of this review is to uncover and organize the findings of such efforts in such a way that provides a better understanding of the implications that selection for marbling may have on maternal productivity. For a review of research that identifies relationships between a number of carcass EPDs and maternal productivity that was published prior to 2008, please reference Twig Marston's Certified Angus Beef LLC white paper entitled "The relationship between marbling and other EPDs with implications when making beef cowherd breeding and management decisions (Marston, 2007)," as the current review will focus on more recent developments that have been reported following Dr. Marston's original review.

Recent developments in this field have focused on identifying relationships between marbling and the major traits that are typically utilized by cattlemen as measurements or indicators of fertility and maternal productivity. These traits, listed in the order in which they will appear throughout this review, include age at puberty and scrotal circumference, heifer pregnancy and age at first calving, birth weight and calving ease, maternal milk, calving interval, stayability and longevity, docility and mature size, as well as feed efficiency and cow-calf profitability indices. Additionally, the review includes an analysis of relationships between marbling and maternal traits that exist amongst sires included in the most recent version of the American Angus Association's Sire Evaluation Report.

Age at puberty and scrotal circumference

One of the major traits that has long been considered an indicator of fertility not only for a sire (Hahn et al., 1969; Almquist et al., 1976; Sitarz et al., 1977), but also for his daughters (Morris et al., 1992; Morris and Cullen, 1994; Vargas et al., 1998), has been scrotal circumference, as scrotal circumference is generally thought of as being highly correlated with pubertal traits (Gregory et al., 1991). Much of the early work in this area supports the notion that scrotal circumference has a moderate phenotypic[1] and relatively high genetic[2] correlation with growth traits such as weaning weight, yearling weight and average daily gain of bulls (Latimer et al., 1982; Knights et al., 1984; Bourdon and Brinks, 1986; Smith et al., 1989a; Kriese et al., 1991) and their progeny (Smith et al., 1989b; Moser et al., 1996). Martinez-Velazquez et al. (2003) found these correlations to be lower than had been previously reported, and went on to suggest that selecting for scrotal circumference may not be as advantageous in selecting for heifer fertility as was once thought. Nonetheless, selection for scrotal circumference remains the major trait utilized by producers for both phenotypic and genetic selection for fertility.

Latimer et al. (1982) were the first to evaluate the relationship between yearling scrotal circumference and ultrasound measured carcass traits and reported that yearling scrotal circumference was not significantly correlated with subcutaneous fat thickness or *Longissimus dorsi* muscle area. It was not until Stelzleni et al. (2003) reported a small relationship between sire scrotal circumference and ultrasound predicted intramuscular fat percentage of Brangus heifer progeny that researchers became interested in the impact that sire selection for scrotal circumference may have on the marbling potential

[1]A phenotypic correlation represents the shared proportion of variation resulting from an interaction between an animal's genotype and the environment.
[2]A genetic correlation represents the proportion of variation resulting from only an animal's genotype.

of their progeny. It is important to note, however, that this relationship was not evaluated statistically by Stelzleni et al. (2003) due to sample size limitations. More recently, McAllister et al. (2011) reported little to no genetic or phenotypic correlation between scrotal circumference and marbling score or intramuscular fat percentage of Red Angus cattle using data obtained from the Red Angus Association of America that included animals born between 1977 and 2007. These authors went on to describe that simultaneous selection for scrotal circumference and marbling score or ultrasound predicted intramuscular fat percentage would not lead to antagonistic effects. This interpretation suggests that increasing the marbling potential of a cowherd would not impact factors of fertility that are associated with scrotal circumference.

Initial data collected during the first four cycles of the germplasm evaluation at the U.S. Meat Animal Research Center in Clay Center, NE, that utilized a sample population that included genetic contribution from over 20 beef and dairy breeds indicated a very low, negative genetic correlation (-0.04) between age at puberty of crossbred heifers and marbling score of their paternal half-sibling steers (Splan et al., 1998). The authors went on to emphasize the close proximity of this correlation to zero, which can be interpreted as having minimal, if any implications to age at puberty. Interpretation of the results reported by Johnston et al. (2009) suggests no genetic correlation between age or weight at puberty and paternal half-sibling steer carcass marbling score for Brahman and Australian tropical composite cattle.

Multivariate analysis of the most current (Fall 2013) Angus Sire Evaluation Report indicates that there currently appears to be no definite relationship between marbling and scrotal circumference EPDs within the Angus breed. Although inclusion of all sires, regardless of the relative accuracy of their marbling EPD, suggests a low and potentially negligible positive correlation between the marbling and scrotal circumference EPDs (Table 1), inclusion of only high accuracy sires[3] reveals no statistically significant correlation (Table 2). These results support those found in the literature, and their interpretation suggests that producers can select for marbling with little to no impact on scrotal circumference and age at puberty.

Heifer pregnancy and age at first calving

Upon reaching puberty, profitability of a female to a producer can be limited by her ability to conceive during a normal breeding season. As such, age at first calving has traditionally been considered to be the major measurement utilized by both seedstock and commercial producers to quantify this trait. Bergfeld et al. (1995) first reported that heifer progeny of crossbred cows that were sired by high marbling EPD sires did not differ in age at first calving when compared to contemporaries that were sired by low marbling EPD bulls. However, it is important to note that these results were generated using a relatively small sample population. In contrast, results reported by Frazier et al. (1999) that were generated using data obtained from the American Angus Association database indicated a relationship between sire marbling EPD and age at first calving. The authors went on to describe that a single unit increase in sire marbling EPD corresponded with an increase in age at first calving of

[3]High accuracy sires were defined as those with a marbling EPD accuracy of greater than or equal to 0.50 that have 50 or more daughters with progeny weaning weight records (MkD).

approximately 10 days, suggesting that a two-unit increase in sire marbling EPD would be required to extend the age at first calving by the length of a single estrous cycle. Minimum and maximum values reported by the American Angus Association for the marbling EPD suggests a range of 2.24 marbling EPD units across all Angus bulls that were included in the Fall 2013 Sire Evaluation Report. Based on this, a breeder that progresses from the lowest possible marbling extreme to the highest would be expected to extend age at first calving for heifers by approximately twenty-three days. More realistically, a breeder that makes a 0.25 unit improvement in marbling EPD would be expected to increase age at first calving by less than three days.

In contrast to these results, Evans et al. (2004) identified a positive relationship between ultrasound predicted intramuscular fat percentage and heifer pregnancy, as synchronized artificially inseminated crossbred heifers that conceived had a greater percent intramuscular fat (3.09 ± 0.04 vs. 3.01 ± 0.05) when compared to heifers that did not conceive to a single service when ultrasounded 14 days following synchronization. Interestingly, the authors also observed a lower percentage of intramuscular fat (2.93 ± 0.07) for heifers that did not respond to synchronization and were deemed non-cycling. McAllister et al. (2011) reported a negligible genetic correlation (0.10 ± 0.15) between the Red Angus heifer pregnancy EPD and carcass marbling score, and a low correlation (0.13 ± 0.09) with intramuscular fat percentage. While marbling score and intramuscular fat are strongly related, this relationship is not perfect for a number of reasons. As such, there does not appear to be a strong relationship between marbling and the Red Angus heifer pregnancy EPD (McAllister et al., 2011).

In 2011, the American Angus Association began to include a heifer pregnancy EPD as a member of its maternal trait EPD genetic predictions. Although expressed in different units than that of the Red Angus Association, the EPD is intended to achieve the same goal: provide an estimate of the probability that a sire's daughter will become pregnant during a normal breeding season. Recently, the Association reported no genetic correlation between marbling and heifer pregnancy EPDs for sires with an accuracy of equal to or greater than 0.50 (AAA, 2013).

Similar to the results reported by the American Angus Association, multivariate analysis of high accuracy sires evaluated in the Fall 2013 Angus Sire Evaluation Report suggests no statistically significant phenotypic correlation between the marbling and heifer pregnancy EPDs (Table 2). Although selection for marbling may lead to an increase in age at first calving in extreme situations, cattlemen should be capable of selecting for marbling without reducing heifer pregnancy within their herds.

Birth weight and calving ease

Dystocia, commonly referred to as calving difficulty, is a major concern amongst beef producers, as it is considered by many to be the most influential factor affecting calf losses over time. During an already labor intensive time, additional resources devoted to assisting females during parturition, as well as the increased death loss of both calves and heifers or cows associated with dystocia can greatly affect producer profitability. In addition to calf and heifer or cow mortality, dystocia often leads to reduced conception, increased calving interval and reductions in growth performance (Greiner, 2004). Excessive

birthweight is a major contributing factor to dystocia, and as such is commonly used as a reference point for calving ease by commercial cattlemen. A series of experiments conducted in the 70's by Bellows et al. (1971) and Smith et al. (1976) first identified a relationship between birthweight and gestation length of a variety of beef sire breeds. One of the more interesting assumptions related to genetic selection against dystocia has been that through selection for low birthweight, such improvements may be the result of selection for decreased gestation length.

Regardless of whether cattlemen are indeed selecting for decreased gestation length when selecting for birthweight, Angus sires are highly sought after amongst commercial producers due to their ability to excel at calving ease while maintaining or improving carcass traits when compared to a number of other breeds and their composites. As such, one could hypothesize that these traits may be linked. In 1996, Vieselmeyer et al. reported that selection for high and low marbling EPD Angus sires with moderate accuracy had no effect on progeny birth weight and calving difficulty. However, it is important to note that this study consisted of a relatively small sample population. Additionally, Australian researchers reported a negative genetic correlation (-0.826) between birthweight and carcass intramuscular fat percent (Pitchford et al., 2006), suggesting an inverse (beneficial) relationship between marbling potential and birthweight. Although considered to be a lowly heritable trait, these authors also reported a positive phenotypic correlation (0.746) between calf survival and carcass intramuscular fat percent, also suggesting a positive (beneficial) relationship between marbling potential and calf survival. Pacheco et al. (2011), however, more recently reported no effect of yearling heifer ultrasound predicted intramuscular fat percentage on calf birthweight over four subsequent calving seasons.

The American Angus Association currently reports three EPDs that can be utilized by producers in order to enhance their ability to genetically select for calving ease and against dystocia. These EPDs include birth weight, calving ease direct and calving ease maternal. Since their implementation in 2005, the calving ease direct and calving ease maternal EPDs have provided direct estimates of a parent's contribution to calving ease, as the calving ease direct EPD is used to predict the relative contribution of a sire to the percentage of unassisted births for first-calf heifers mated to a particular sire, while the calving ease maternal EPD is used to predict a sire's contribution to the percentage of unassisted births of first-calf heifer daughters. The American Angus Association is not the only nor the first of the breed associations to report numerous EPDs for calving ease, as most breeds commonly utilized in commercial crossbreeding programs throughout the United States currently report their own variation of the birth weight, direct and maternal calving ease EPDs. Although no reports currently exist that evaluate genetic relationships between marbling and any of the calving ease EPDs for purebred Angus cattle, Pendley (2009) reported no effect of Charolais sire calving ease EPD on the marbling score of steer and heifer progeny from Angus-based dams.

Existing reports suggest that producers should not expect an elevation in birthweight or dystocia as a result of selection for marbling, with the possibility of experiencing improvements in calf survival. Regardless of accuracy, the marbling EPD appears to be negatively correlated with birth weight, and positively correlated with the calving ease direct and calving ease maternal EPDs (Tables 1 and 2), suggesting a favorable relationship between marbling and calving ease within the Angus sire population.

Maternal milk

The ability of a producer to match a cow's genetic potential to a production setting is undoubtedly one of the major factors that impacts cow productivity. As such, success or failure in doing so is often capable of leading to the success or failure of an operation as a whole. This concept has received great interest from the industry throughout the past few years as a result of the reduction in forage availability and increased costs for harvested feedstuffs associated with the recent historical drought conditions that impacted much of the U.S. During times of feed resource abundance, traits that allow producers to fully utilize such resources often lead to elevated profitability in the cow-calf sector for producers who market weaned and/or preconditioned calves. When such resources become scarce or relatively expensive, such as throughout much of the drought, or the more recent unexpected blizzard conditions throughout much of the upper Midwest, many of these traits may have become detrimental to producer profitability, and at times, animal survival.

Of the traits most commonly associated with cow productivity and longevity, milk potential has created the greatest concern among producers. Extensive research was conducted in the early 1970s related to the impact of selection for high levels of milk production on growth traits of dairy cattle intended for beef production. Dairy-influenced cattle, however, are often excluded from value-added retail brands. Lewis et al. (1990) first reported no effect of a dam's milk potential on progeny quality grade when dams of beef breed origin were classified to either a high, medium or low group based upon their crossbreed composition. These results were supported by Fiss and Wilton (1993) who reported no relationship between milk yield and marbling in Hereford cattle utilized in typical Canadian rotational crossbreeding systems. In contrast to these results, Aass and Vangen (1997) reported that Norwegian Red bulls selected for high milk yield potential had a greater intramuscular fat percentage when compared to bulls selected for low milk yield potential. In 1999, Gosey reported that breeds typically recognized for high milk production tend to have greater marbling scores when compared to breeds that are typically recognized for low milk production, but went on to explain that there appeared to, at that time, be no relationship between marbling and milk production within the Angus breed. However no peer-reviewed reports exist that evaluate the potential factors contributing to the nature of this observation amongst breeds.

In 2003, Casas et al. hypothesized that genes residing within a common quantitative trait loci may be involved in a number of metabolic or physiological processes, and as a result may have lasting implications to animal production. In the same year, Thaller et al. (2003) reported the presence of the gene that encodes diacylglycerol-*O*-acyltransferase (DGAT1), an enzyme involved in milk fat synthesis, within what was considered to be the region of the marbling quantitative trait loci on chromosome 14. These authors went on to describe that German Holstein cattle with the homozygous lysine/lysine genotypic polymorphism[4] at the K232A position of the DGAT1 gene have a greater solvent extracted intramuscular fat percentage in both the *Longissimus dorsi* and *Semitendinosus* muscles when compared to a combination of cattle with either the heterozygous lysine/alanine or homozygous alanine/alanine polymorphism (Thaller et al., 2003). The homozygous K232A lysine/lysine polymorphism was later shown to result in a five-fold increase in diacylglycerol-*O*-acyltransferase activity in the *Longissimus dorsi*

[4]The polymorphism that results in the lysine/lysine substitution is commonly referred to as the K232A single nucleotide polymorphism (SNP).

muscle when compared to the heterozygous lysine/alanine and homozygous alanine/alanine polymorphisms (Sorensen et al., 2006). Although Pannier et al. (2010) reported results that were in numerical agreement with the results reported by Thaller et al. (2003), the reported differences related to the K232A polymorphism remained statistically insignificant. Later, Anton et al. (2011) observed similar results in Hungarian Angus cattle as were observed in German Holsteins by Thaller et al. (2003). These reports were most recently confirmed for Swedish Angus bulls by Li et al. (2013). However, no reports currently exist that evaluate the prevalence of the K232A single nucleotide polymorphism for Angus cattle within the U.S.

Additionally, researchers within the dairy community have provided evidence that the K232A single nucleotide polymorphism is associated with negligible reductions in uncorrected milk yield of Scottish Holsteins (Banos et al., 2008), but major elevations in fat yield of Dutch Holsteins that correspond with minor reductions in protein yield (Streit et al., 2011). Similar effects were reported for daughter yield deviations in milk, fat and protein yield of Holstein sires (Barbosa da Silva et al., 2010). Although reports of the relationship between marbling and milk production have been relatively inconsistent, genomic research has provided more clear evidence of a relationship between milk production and marbling potential through DGAT1. As such, one must keep in mind that this relationship represents only a small portion of a parent's genetic contribution toward milk production.

These effects, however, appear to be unique to *Bos taurus* cattle, as Casas et al. (2005) and Curi et al. (2011) reported no relationship between the K232A polymorphism and marbling score or percent intramuscular fat of Brahman or Nellore cattle, respectively.

Although the relationship cannot be ignored, the proportion of the populations in which the lysine/lysine mutation occurs is small for Swedish and Hungarian Angus sires, ranging from 2 (Li et al., 2013) to 5 (Anton et al., 2011) percent, respectively, the potential implications of selecting for individuals that possess this polymorphism should not be ignored. Additional research is necessary in order to determine the prevalence of this polymorphism in American Angus cattle, and determine the presence or absence of any relationships that may exist between the marbling and milk EPDs of Angus parents possessing the polymorphism.

Regardless of sire accuracy, there currently appears to be a positive phenotypic correlation between the marbling and maternal milk EPDs amongst Angus sires (Tables 1 and 2). These findings support a number of those reported throughout the literature. The impact that this relationship may have in a cow-calf setting, however, is operation dependent, and primarily based upon feed resource availability. Additionally, interpretation of the results of a multivariate analysis of the 25 most popular[5] Angus sires included in the Fall 2013 Angus Sire Evaluation Report indicates that this relationship may be higher for sires whose daughters have been retained extensively throughout purebred herds and sons that are prevalent in commercial herds (Table 3). This interpretation suggests that single-trait selection for marbling may lead to elevations in maternal milk yield. However it is difficult to differentiate whether this relationship is the result of single trait selection for marbling, or simultaneous selection for elevations in both marbling and maternal milk. Nonetheless, it is important to note that opportunity

[5]Sires were ranked from greatest to least in terms of the number of daughters for which the American Angus Association has progeny weaning weight records.

currently exists within the Angus sire population to select for marbling while divergently selecting for maternal milk. As such, producers should remain cognizant of this relationship while making selection decisions, and as always, are encouraged to avoid single trait selection.

Calving interval, stayability and longevity

Calving interval is often a major concern amongst cattlemen. Aside from feed costs, investments associated with retaining or purchasing and developing replacement females are often one of the greatest expenses encountered by a cow-calf producer. After considering these costs, maternal reproductive efficiency remains one of the most important aspects to a cow-calf enterprise (Frazier et al., 1999), as both replacement heifers and mature females are often culled due to their inability to become pregnant during a normal breeding season. Although Frazier et al. (1999) reported no relationship between Angus sire marbling EPD and second or mature calving interval of Angus cows, the authors reported that sire marbling EPD was favorably associated with the number of days between first and second calving. Although sire marbling EPD explained less than two percent of the variation in first calving interval, a single unit increase in sire marbling EPD corresponded with a 24 day decrease in first calving interval (Frazier et al., 1999). In 2011, Pacheco et al. reported no effect of yearling ultrasound predicted intramuscular fat percent of Angus-cross heifers on calving interval throughout the following three years. These results support the notion that marbling potential does not have a negative impact on calving interval.

In 1993, the Red Angus Association of America began to publish an EPD for stayability. Those efforts were then followed by the American Simmental Association, which began to report a similar EPD in 2006. Aimed at providing an indication of cow longevity, the stayability EPD provides a relative indication of the probability that a female will remain within a herd for six years[6] or more, given that she calved as a two year old. Soon after the development of the stayability EPD, the American Simmental Association reported negative genetic correlations between stayability and both milk (-0.15) and marbling (-0.19) EPDs (Shafer, 2007). No peer-reviewed reports currently exist in the literature that have evaluated this relationship in a similar manner. Although the American Angus Association has expressed its intention of including a stayability EPD as a member of its maternal EPD collection, no such value currently exists.

Based on the results reported in the literature, producers should expect no negative impact on calving interval as a result of selection for marbling, with the possibility of observing a favorable numeric reduction. Research is necessary in order to better understand the implications that selection for marbling may have on stayability, and to determine if this effect is independent of breed, or indeed unique to Simmental cattle. Nonetheless, the Simmental breed remains a popular option for both seedstock and commercial producers in two-breed rotational crossbreeding systems. As such, producers should remain cognizant of the relationship between the marbling and stayability EPDs reported by the American Simmental Association when making Angus-Simmental crossbreeding selection decisions.

[6]Six years is considered by the American Simmental Association to be the predicted age at breakeven for a replacement female.

Docility

Docility is another trait that impacts the potential longevity of a female in a cowherd, as aggressive females pose a liability risk and are often culled based on their disposition. Maternal behavior is partially thought to be under genetic control, presenting opportunity for the trait to be selected for when making breeding decisions (Grandinson, 2005). Phocas et al. (2006) reported a negative genetic correlation between docility score and age at puberty, and a positive genetic correlation between docility score and calving rate after timed-AI for Limousin heifers. Although interpretation of these results suggests a favorable relationship between docility and fertility, Beckman et al. (2007) reported low maternal heritability estimates for the disposition of Limousin cows using chute-side temperament scores. The authors went on to report that maternal genetic and environmental effects were capable of explaining only eight percent of the phenotypic variation in temperament scores (Beckman et al., 2007). In support of these results, Hoppe et al. (2008) reported a low phenotypic correlation between postpartum maternal behavior and calf weaning weight or average daily gain of German Angus cattle.

The majority of research that has evaluated the implications of temperament on production traits has been collected on finishing cattle. Busby et al. (2006) reported that docile calves were heavier upon arrival at the feedyard, and had greater average daily gain throughout finishing, as well as higher quality grades and increased acceptance to the Certified Angus Beef ® retail brand when calves were categorized as docile, restless, or aggressive based on cumulative temperament scores measured at three time points throughout finishing. Additionally, results of an economic analysis revealed that docile calves had greater financial returns when compared to aggressive calves (Busby et al., 2006). The relationship between docility and quality grade reported by Busby et al. was later supported by Hall et al. (2011) who reported a moderately negative correlation between aggressiveness and marbling when disposition was measured immediately following restraint in a head-chute.

Based on these relationships, as well as the low to moderate heritability of disposition, one could hypothesize that a genetic relationship may exist between docility and marbling. However, no peer-reviewed reports currently exist that can prove or disprove this hypothesis when evaluated from solely a genetic perspective. Nonetheless, there currently appears to be a favorably positive phenotypic correlation between the marbling and docility EPDs within the Angus breed regardless of sire accuracy (Tables 1 and 2), suggesting that selection for marbling may lead to more docile females.

Mature size

Mature cow size is often considered by producers to be an important factor when making breeding decisions, as increases in size are generally thought to be expensive from a maintenance energy perspective. In contrast, larger mature cow size may enhance revenue through a positive association with growth traits as well as cull cow weight. As such, preference for mature cow size varies across producer, and is highly dependent upon individual management and marketing scenarios.

Nonetheless, reports of research evaluating the implications of cow size on carcass traits remain scarce, Nephawe et al. (2004) reported low negative genetic correlations between differential measures of mature cow body size and steer progeny marbling score for cattle involved in the first four cycles of the Germplasm Evaluation Program at the U.S. Meat Animal Research Center.

Although there currently appears to be no statistically significant phenotypic correlation between the marbling and mature weight EPDs across all Angus sires included in the Fall 2013 Sire Evaluation Report (Table 1), marbling appears to be positively correlated with mature height of high accuracy Angus sires (Table 2). Interpretation of these results suggests that single trait selection for marbling will result in taller, larger framed mature females within a herd. However the lack of a statistically significant phenotypic correlation between marbling and mature weight EPDs makes the potential impact of this relationship difficult to interpret.

Feed efficiency and cow-calf profitability indices

Feed costs typically make up the majority of the expenses that a cow-calf enterprise incurs. As such, selection for feed efficiency without sacrificing other traits enhances profitability. Due to the extensive interest in this field, a number of methods have been developed that are utilized throughout the industry to measure feed efficiency. Although each method has its own benefits and limitations, residual feed intake currently appears to be the most popular method of evaluating feed efficiency within the animal science research community, and has been adopted by a number of sire test facilities. Residual feed intake, or the difference between observed and predicted feed intake, provides a relative estimate of efficiency after adjusting an animal within a population to a similar body weight, average daily gain and body composition to its contemporaries. In contrast to a number of measurements for feed efficiency, a lower, or more negative value for residual feed intake is desirable, as such a value indicates that an animal consumed a relatively lesser amount of feed in order to achieve a similar average daily gain after being adjusted to a similar body weight and composition that reflects the average of its contemporaries. As such, a negative correlation between marbling and residual feed intake would be considered to be a desirable relationship.

Over the past decade, a number of researchers have attempted to identify potential relationships between residual feed intake and carcass characteristics, while primarily focusing their efforts on performance tested bulls and finishing cattle. Basarab et al. (2003) first reported a positive phenotypic correlation (0.22) between finishing residual feed intake and change in marbling score throughout the finishing phase, suggesting the presence of a relationship between the two traits. Although Schenkel et al. (2004) reported no genetic correlation between residual feed intake and ultrasound predicted intramuscular fat percentage utilizing data collected from purebred bulls at the Ontario bull test station, Robinson and Oddy (2004) reported a positive phenotypic correlation (0.22) between residual feed intake and near infrared spectroscopy predicted intramuscular fat percent of tropically and temperately adapted Australian finishing cattle. After classifying Angus steers as either high, medium or low for residual feed intake, Baker et al. (2006) reported no effect of residual feed intake on carcass marbling

score. Nkrumah et al. (2007) reported a positive phenotypic correlation between carcass marbling score and both phenotypic (0.17) and genetic (0.14) measurements of residual feed intake of crossbred steers sired by Angus, Charolais and Alberta Hybrid bulls. However, no relationship existed between ultrasound predicted marbling score and RFI in the same study.

Although the above results were reported for bulls in a performance test or steers and heifers in a finishing scenario, one would intuitively expect the results to be similar for females developed in a replacement scenario. Crews (2005) reported that residual feed intake is a moderately heritable trait, with a heritability ranging from 0.26 to 0.43. This range in heritability is considered to be similar to that of many carcass traits (Nkrumah et al., 2007), and can be interpreted to signify that a moderate portion of the variation in progeny residual feed intake can be explained by parental genetics. Based on this concept, one would expect selection for improvements in marbling to potentially lead to elevations in residual feed intake, which correspond with reductions in feed efficiency. Lancaster et al. (2009) reported a tendency toward a linear reduction in ultrasound predicted intramuscular fat percentage at the beginning of the intake measurement period as residual feed intake classification progressed from low to medium and high for Brangus heifers. Although numerical differences in ultrasound predicted intramuscular fat percentage followed the same trend at the end of the intake measurement period, the tendency toward significance was lost, while the change in intramuscular fat throughout the intake measurement period remained unaffected by residual feed intake classification (Lancaster et al., 2009). Shaffer et al. (2011) reported no effects of high, medium, or low RFI classification on ultrasound predicted intramuscular fat percentage of yearling Angus, Angus-cross and Hereford replacement females when measured at the initiation and conclusion of an 84 (year one) and 71 (year two) day development period. The authors also reported no effects of RFI classification on marbling development when expressed as a change in percent intramuscular fat throughout the duration of the development program, and went on to report no phenotypic correlation between residual feed intake and initial, final, or change in ultrasound predicted intramuscular fat percentage irrespective of RFI classification (Shaffer et al., 2011).

Archer et al. (2002) reported a moderate phenotypic correlation between residual feed intake measured for growing Australian Angus heifers divergently selected for residual feed intake and measured again as mature, 3-year old non-lactating cows that received identical rations across measurement periods. More recent work published by Kelly et al. (2010) supports these results, and suggests that residual feed intake measured throughout the growing phase is moderately repeatable when measured again throughout finishing. Although the limited number of existing reports support the notion that a moderate relationship exists between the relative efficiency of a growing heifer and her efficiency measured as a lactating cow, Durunna et al. (2012) provided evidence of re-ranking amongst crossbred replacement heifers across two consecutive growing phases throughout which heifers received similar diets. However, U.S. producers typically develop replacement females utilizing separate nutritional management strategies than are utilized to support mature cowherds. After incorporating these differences in management strategies, Black et al. (2013) reported no significant correlation between residual feed intake measured during development and again as a 3-year old lactating cow. Interpretation of these results suggests that females that are considered to be relatively efficient

throughout development may not necessarily be the most efficient later in life. Additionally, limitations associated with the difficulty in evaluating feed efficiency of mature females in a grazing setting has left a void in the ability of researchers to identify relationships between early marbling development and the relative feed efficiency of mature females.

In 2010, the American Angus Association began reporting a residual average daily gain EPD. Although calculated differently, the residual average daily gain EPD serves a similar purpose as residual feed intake, but instead focuses on average daily gain rather than feed intake. As such, the measurement is generally considered to be more applicable across sample populations, and thus have more utility as a selection tool. During the development of the residual average daily gain EPD, MacNeil et al. (2011) utilized a combination of individual feed intake, weaning weight, post-weaning bodyweight gain and ultrasound predicted subcutaneous fat depth in order to provide an estimate of expected progeny post-weaning feed efficiency for animals that received a similar type and amount of feed (Northcutt and Bowman, 2010). In contrast to estimates of residual feed intake, a positive estimate for residual average daily gain is considered to be beneficial, as positive measurements correspond to a greater than expected average daily gain. No peer-reviewed reports currently exist that evaluate relationships between residual average daily gain and carcass traits. Nonetheless, the marbling EPD currently appears to be positively correlated with the RADG EPD (Tables 1 and 2) amongst Angus sires, suggesting a favorable relationship between marbling potential and post weaning gain efficiency.

In addition to the residual average daily gain EPD, the American Angus Association currently includes two $Value indices as a component of its sire evaluation; cow energy value ($EN) and weaned calf value ($W). Although not direct measures of efficiency, these indices are intended to provide cow-calf producers with the opportunity to more easily incorporate multi-trait selection decisions into their breeding program.

The cow energy value index reported by the American Angus Association provides an estimation of the economic savings of female progeny that can be attributed to differences in energy requirements. Specifically, the components of this index include predicted energy requirements for lactation, as well as mature cow size (Northcutt, 2009). Based on the relationships that exist between the marbling and maternal milk EPDs, as well as the marbling and mature height EPDs within the Angus breed, one would expect a relationship to exist between marbling and $EN. Although no peer-reviewed publications exist that evaluate the presence or absence of such relationships, there currently appears to be an undesirable negative phenotypic correlation between the marbling EPD and $EN index within the Angus breed, regardless of sire accuracy (Tables 1 and 2). This relationship appears to be numerically greater (more undesirable) amongst the 25 most popular bulls that have sired females that have been retained in purebred herds (Table 3). Based on this antagonistic relationship, one may initially arrive at the conclusion that cows with a high genetic propensity for marbling are relatively energetically expensive to maintain based on their $EN. Similar to the relationship between marbling and milk yield, the degree of impact that this relationship may have in a cow-calf setting is dependent upon the abundance and quality of feed resources utilized to support the cowherd. Additionally, it is important to note that

opportunity currently exists within the Angus breed to select for marbling while utilizing sires with a favorable $EN index.

With an overall goal of characterizing cow-calf profitability at weaning, the $W index provides an expected difference for pre-weaning progeny performance that is expressed in the form of a dollar value. Although relationships between the $W index and the marbling EPD within the Angus breed have not been evaluated, there currently appears to be a favorably positive phenotypic correlation between the two, regardless of sire accuracy (Tables 1 and 2). Interpretation of results reported in Table 3 suggests that this relationship may be numerically greater amongst the 25 most popular Angus sires.

The conflicting results obtained for relationships between the marbling EPD and the $W or $EN indices suggest that the negative correlation between the marbling EPD and $EN index may be a result of the relationship that exists between marbling and maternal milk. Based on this, it is advisable that cattlemen remain cognizant of this relationship. Divergent selection for improvements in marbling that optimizes milk yield potential in such a way that matches a female's genetic potential to a producer's management scenario (i.e. feed resource abundance) may negate the impact of the relationship between the marbling EPD and $EN index. Additionally, divergent selection efforts may be capable of negating this relationship altogether.

Conclusion and closing remarks

Interpretation of existing reports suggests that selection for marbling will not negatively impact many traits that are considered important for maternal productivity. This literature review, along with the results of an analysis of the American Angus Association Sire Summary, supports a positive, albeit relatively low, association between marbling and milk within the Angus breed. This direct correlation appears to be much higher amongst the most heavily used Angus sires (based upon number of daughters). However, it is important to note that a relationship does not affirm causation, as simultaneous selection pressure for different traits can create potentially unfavorable relationships, which could help to explain some negative perceptions associated with selection strategies that include elevations in marbling, even within balanced-trait selection. Additionally, this notion could suggest that these perceptions are the result of elevations in milk that have simultaneously been bred into certain high marbling Angus sires, as level of milk production can impact cow body condition and rebreeding rate. Additional genomic and applied research and analysis of U.S. beef cattle populations is necessary in order to more effectively characterize these relationships, as well as to identify the presence or absence of a genetic link between these traits. Nonetheless, their impact will remain largely dependent upon individual production scenarios, both in terms of selection pressure for marbling, and feed resource availability to support its related traits. In closing, these observations reiterate the importance of balancing trait selection in such a way that matches the genetic potential of a cowherd to a producer's feed resources and marketing strategies, or for producers possessing the ability and opportunity, the utilization of segregated nutritional management scenarios within a cow-calf enterprise.

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Rob and Lori Thomas – Thomas Angus Ranch
Alison Van Eenennaam – University of California, Davis
Bob Weaber – Kansas State University
Kevin Yon – Yon Family Farms

Table 1. Pairwise correlations between marbling and maternal EPDs or $Value indices for all sires included in the Fall 2013 Angus Sire Evaluation Report

	Statistics	
EPD or $ Index	r	*P* - value
Birth Weight (BW)	-0.08	0.0001
Calving Ease Direct (CED)	0.17	< 0.0001
Calving Ease Maternal (CEM)	0.28	< 0.0001
Weaning Weight (WW)	0.15	< 0.0001
Yearling Weight (YW)	0.19	< 0.0001
Residual Average Daily Gain (RADG)	0.07	0.0027
Scrotal Circumference (SC)	0.06	0.0039
Heifer Pregnancy (HP)	0.06	0.0408
Docility (DOC)	0.05	0.0258
Maternal Milk (Milk)	0.22	< 0.0001
Mature Weight (MW)	0.13	< 0.0001
Mature Height (MH)	0.18	< 0.0001
Cow Energy Value ($EN)	-0.23	< 0.0001
Weaned calf Value ($W)	0.15	< 0.0001

Table 2. Pairwise correlations between marbling and maternal EPDs or $Value indices for high accuracy sires[1] included in the Fall 2013 Angus Sire Evaluation Report

	Statistics	
EPD or $ Index	r	*P* - value
Birth Weight (BW)	-0.12	0.0279
Calving Ease Direct (CED)	0.17	0.0018
Calving Ease Maternal (CEM)	0.28	< 0.0001
Weaning Weight (WW)	0.25	< 0.0001
Yearling Weight (YW)	0.28	< 0.0001
Residual Average Daily Gain (RADG)	0.20	0.0001
Scrotal Circumference (SC)	--	0.1775
Heifer Pregnancy (HP)	--	0.9077
Docility (DOC)	0.13	0.0164
Maternal Milk (Milk)	0.23	< 0.0001
Mature Weight (MW)	--	0.2917
Mature Height (MH)	0.14	0.0100
Cow Energy Value ($EN)	-0.24	< 0.0001
Weaned calf Value ($W)	0.26	< 0.0001

[1]Includes all Angus sires with a marbling EPD that was greater than or equal to 50 percent accuracy and an MkD value of greater than 50

Table 3. Pairwise correlations between marbling and maternal EPDs for the 25 most popular sires[1,2] that were included in the Fall 2013 Angus Sire Evaluation Report

	Statistics	
EPD or $ Index	r	*P* - value
Birth Weight (BW)	--	0.6629
Calving Ease Direct (CED)	--	0.1200
Calving Ease Maternal (CEM)	--	0.2764
Weaning Weight (WW)	0.46	0.0211
Yearling Weight (YW)	0.50	0.0114
Residual Average Daily Gain (RADG)	--	0.4669
Scrotal Circumference (SC)	--	0.4357
Heifer Pregnancy (HP)	--	0.1694
Docility (DOC)	0.36	0.0759
Maternal Milk (Milk)	0.53	0.0069
Mature Weight (MW)	--	0.1880
Mature Height (MH)	--	0.2120
Cow Energy Value ($EN)	-0.40	0.0468
Weaned calf Value ($W)	0.55	0.0042

[1]Popularity was defined by the number of daughters with progeny weaning weight records (MkD).

[2]MkD values ranged from 18,264 to 5,543 for the 25 most popular Angus sires.

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