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Genetic Parameters For Docility, Weaning Weight, Yearling Weight And Intramuscular Fat Percentage In Hereford Cattle

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GENETIC PARAMETERS FOR DOCILITY, WEANING WEIGHT, YEARLING WEIGHT AND INTRAMUSCULAR FAT PERCENTAGE IN HEREFORD CATTLE

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Temperament in cattle can be described as the reactivity or fear response to human handling, and it is important to beef cattle producers not only from a human safety but also due to potential correlations with other economically traits. Before a docility selection metric can be added to a genetic evaluation, any potential antagonisms with economically relevant traits should be quantified. The objective was to estimate genetic parameters, including genetic correlations, for chute score (CS), weaning weight (WW), yearling weight (YW), and intramuscular fat percentage (IMF) in Hereford cattle. Single-trait and bivariate animal models were used to estimate heritabilities and genetic correlations. Models included fixed effects of sex and contemporary group, defined as herd–year–season. Direct genetic and residual components were included as random effects. For CS and WW, also additional random effects of maternal genetic and maternal permanent environment were fitted. For CS, WW, YW, and IMF, heritability estimates were 0.27 ± 0.02, 0.35 ± 0.03, 0.36 ± 0.02, and 0.27 ± 0.02, respectively. Genetic correlations between CS and WW, CS and YW, CS and IMF, WW and YW, WW and IMF, and YW and IMF were –0.12 ± 0.06, –0.10 ± 0.05, –0.08 ± 0.06, 0.47 ± 0.05, –0.19

± 0.09, and –0.41 ± 0.05, respectively. Heritability estimates for all traits suggest that they would respond favorably to selection, although the selection for increased WW or YW could decrease marbling, which is often associated with favorable meat quality. Genetic correlations between CS and WW, YW, and IMF were all favorable but weak, suggesting that selection for improved docility will not have negative consequences on growth or meat quality. Maternal additive and maternal permanent environmental variances for CS were close to zero, suggesting that their inclusion in National Cattle Evaluations is not warranted.

Dedication

I dedicate my thesis work to my wife Mireya Coronel Botello and my daughter Samantha Torres Coronel, whose words of encouragement motivated me until close this process. A special feeling of gratitude to my loving parents, Jose Antonio and Ofelia, because without their love and patience, I would have not closed this process. I also dedicate this thesis to my sister Claudia, my niece Romina and my nephew Diego, for all the support given to me.

Content

Introduction

Cattle temperament or docility is defined as the behavioral response of the animal being handled by humans, and can be assessed using several methods (Burrow, 1997). Docile cattle are referred to as good temperament, while the opposite are referred to as aggressive animals or animals with poor temperament (Petherick et al., 2002). One of the challenges is to find a measure that adequately represents this trait, because temperament is assumed to be multidimensional and involve behavioral characteristics like shyness-boldness, exploration avoidance, activity, sociability and aggressiveness (Haskell et al., 2014; Réale et al., 2007).

It is well documented that cattle vary in their response to stressors and environmental changes. In fact, overly aggressive animals are considered as undesirable given potential safety risks to human handlers and these cattle are prone to be culled (Cafe et al., 2011a; Turner et al., 2011). Conversely, calm temperament has been associated with increased ADG, health, meat quality and superior responses to infections, which improves overall herd productivity (Burrow, 1997; Fell et al., 1999; Kadel et al., 2006). Moreover, temperament traits are important because feedlot managers and producers would suggest that excitable cattle could be more costly to raise in terms of required handling time, labor, and equipment repair (Hall et al., 2011). Due to the associations between temperament and production traits, assessment of beef cattle temperament has increased in recent years (Norris et al., 2014). Consequently, several breed associations are now routinely scoring and recording docility to include in National Cattle Evaluations (Beckman et al., 2007;

Norris et al., 2014). The phenotype that is currently used in National Cattle Evaluations is the subjective measure of chute score (Beef Improvement Federation, 2010).

Despite the fact that several authors have reported associations between temperament traits and economically relevant traits, there is not a general consensus relative to these associations because these results could vary due to several different factors (e.g., method of evaluating docility, rearing conditions, breeds, etc.) (Haskell et al., 2014; Norris et al., 2014). Even though several breed associations are now routinely measuring docility to include in beef selection programs (Beckman et al., 2007; Norris et al., 2014), any potential antagonisms with economically relevant traits should be quantified to ensure selection to improve docility will not erode progress made in economically relevant traits. Once successfully implemented, selection programs to improve docility in cattle could result in a positive benefit to improve animal performance, human safety and animal welfare (Norris et al., 2014).

Literature Review

Classification and measurement of temperament in beef cattle

Several techniques have been used in cattle to measure docility, ranging from simple visual observations to computerized techniques (Norris et al., 2014). Some methods for scoring temperament in cattle production were developed in the early 1960's (Strickin and Kautz-Scanavy, 1984). According to Friedrich et al. (2015), assessment of temperament in cattle was adapted from behavioral studies of laboratory rodents and can be classified based on the type of test (restrained or non-restrained), the data assessment (during routine handling or specific test conditions), and trait type (qualitative or quantitative). In beef cattle, the most common way to classify these methods is categorizing them into restraint techniques, non-restraint techniques and phenotypic evaluations (Burrow, 1997; Norris et al., 2014). Restraint techniques evaluate temperament when animals are physically restricted in a handling chute or confined in a pen, or by measuring the response by assessing the time to move away from the place of confinement; most commonly tests in this category use subjective assessments of behavior assigned by the observer (Burrow and Corbet, 2000; Haskell et al., 2014). Non-restrained techniques refer to methods when the animal is not confined, and cattle temperament is scored by their fear or aggressive response to humans when they are free to move within a relatively large evaluation area. Phenotypic evaluations usually refer to indirect measures of docility, assessing external features of cattle that have been associated with temperament (Burrow, 1997; Cooke, 2011; Norris et al., 2014).

Assessment of docility in cattle

In beef cattle, temperament is usually scored during weighing when cattle are restrained. The main assessments in the restrained category includes chute score and flight time (Norris et al., 2014; Friedrich et al., 2015; Haskell et al., 2014); while the most commonly used non-restrained temperament test includes pen score (Cooke, 2011; Haskell et al., 2014; Norris et al., 2014). Although there are other open field tests in this category where animals are free to move within a defined testing area, these tests are usually applied in dairy cattle (Friedrich et al., 2015). Despite the fact other methods have been reported in both categories to assess temperament in beef cattle, the tests mentioned above have been shown to be the most commonly used, perhaps because they are simple to carry out during handling procedures (Cooke, 2011).

There is no preferred test because each method has some limitations (Randel et al., 2012). However, in order to choose the type of test to assess docility, the management conditions in beef cattle could dictate the type of test used. Phocas et al. (2006) mentioned that in Europe, cattle management conditions are less extensive than in the United States or Australia and therefore cattle are more accustomed to direct handling by humans, thus cattle may not exhibit significant variations for temperament in a docility score or chute score. In addition to this, other aspects should be considered to choose the appropriate assessment. For instance, the feasibility and ease of obtaining the measurement, cost or infrastructure on farms may dictate the temperament test used (Sant'Anna et al., 2013). In addition, Curley et al. (2006), suggested that a useful tool for discerning cattle temperament must be reliable, repeatable, and linked to the individual animal's stress responsiveness. In beef cattle, the most commonly used temperament assessments are:

Docility score or Chute score is commonly referred to as crush score in Australia and Europe. Animals are individually restrained in the chute and scored on a 1-6 scale according to their behavior (Haskell et al., 2014). According to this classification, animals with scores of 1 are considered docile or calm; score 2 indicates animals that are restless or shifting; score 3 indicates animals that are squirming or nervous; score 4 indicates animals that are flighty (wild); and scores 5 and 6 represent aggressive and very aggressive animals, respectively (Grandin, 1993; Beef Improvement Federation, 2010). This assessment is easy to use as calves are routinely handled for management at weaning or yearling ages and is positively correlated with other measures of temperament, but not correlated with cortisol concentrations in blood (Randel et al., 2012).

Flight speed or flight time was proposed by Burrow et al. (1988), and objectively measures the time it takes to cover a set distance along a raceway from the time an animal is released from a chute with high velocity indicating poor temperament (Burrow et al., 1988; Haskell et al., 2014). Usually the distance is short to capture the immediate response and can be referred to as **exit velocity** (Cafe et al., 2011a; Haskell et al., 2014). The objective measure is performed automatically using an electronic device (Curley et al., 2006; Müller and von Keyserlingk, 2006), and according to Norris et al. (2014), the standard distance to measure velocity is over 6 feet (1.83 meters). One electronic trigger is placed in front of the squeeze chute, within 6 feet, and the second trigger is placed 6 feet from the first, and the elapsed time is converted to velocity by dividing the distance by the elapsed time (Beef Improvement Federation, 2010; Randel et al., 2012). According to Randel et al. (2012) a positive aspect for this assessment is that it is an objective measurement without the bias from the observer. Exit velocity also can be expressed on a 1-6 scale, where 1 indicates slow animals and 6 refers to very fast animals. This scale was suggested as an easy and inexpensive alternative to purchasing infrared sensor equipment (Lanier and Grandin, 2002; Vetters et al., 2013).

Pen score is a subjective measurement in which cattle are separated into small groups (from 3 to 5 animals) and then scored relative to their reactivity to a human observer (Grandin, 1993; Hammond et al., 1996). According to this classification, score 1 represents animals unalarmed and unexcited that walk away from the observer; score 2 indicates slightly alarmed cattle that trot away from the observers; score 3 indicates moderately alarmed and exited animals; and scores 4 and 5 represent excited and very excited animals, respectively (Cooke, 2011; Norris et al., 2014). The last category also includes animals that act in an aggressive manner that could require evasive actions by the evaluator to avoid contact (Norris et al., 2014). This test is recommended to perform near weaning to avoid the adaptation of cattle to repeated handling (Curley et al., 2006; Randel et al., 2012). According to Randel et al. (2012), the test measures different behaviors than are measured by the docility or chute score; and contrary to other tests, pen scores are more highly correlated with cortisol concentrations in the blood.

Several authors have reported measures of temperament to be repeatable (Curley et al., 2006; Haskell et al., 2014). For example, results from Kadel et al. (2006), suggested that the ranking of animals based on genetic predisposition for temperament is consistent over time. The average age of cattle at the first and second recordings was 246 and 564 days. These authors reported genetic correlations across measurement times for flight time (0.98) and crush score (0.96) measured over time, indicating a strong underlying genetic basis of these traits. Although some authors have reported significant associations between different techniques, suggesting that a large portion of the genes underlying one measure of docility also underlie other measures of docility (Hoppe et al., 2010; Café et al., 2011a; Sant'Anna et al., 2013; Haskell et al., 2014), others have not found these associations, suggesting that the different methodologies assess different aspects of behavior (Grandin, 1993; Kilgour et al., 2006; Sant'Anna et al., 2015). Fordyce et al. (1988), assumed that animals accustomed to being handled in a paddock could behave differently when they are in a restrained situation; consequently, it is not always possible to relate temperament in restrained situations with non-restrained situations. According to Sant'Anna et al. (2013) there is not a consensus regarding the ideal approach that should be applied for on-farm assessments to measure docility, and few authors have compared the advantages and disadvantages of the different assessment of temperament in beef cattle genetic evaluations (Kadel et al., 2006).

Hormonal factors of docility

Plasma cortisol concentrations and other metabolite concentrations, mainly glucose and lactate, have been significantly associated with poor temperament (Stahringer et al., 1990; Cafe et al., 2011b). Cafe et al. (2011b) suggested that more excitable animals show greater activation of the hypothalamic-pituitary-adrenal axis resulting in the production of more cortisol and glucose, and several authors have found that lower levels of cortisol are associated with higher growth rates (Purchas et al., 1980). However, the underlying physiological explanation between the associations of temperament with other economically important traits is not well documented in beef cattle (Sant'tAnna et al., 2015). Not all temperament tests have been found to be related with serum concentration of cortisol in the blood. For instance, Curley et al. (2006) did not find an association between chute score and cortisol concentrations in blood. The authors did report that pen score measures and exit velocity were phenotypically correlated with cortisol concentrations in the blood ($r = 0.29$, and $r = 0.26$, respectively), suggesting that exit velocity measures may be more useful as indicator of temperament through an animal's lifetime, than subjective measures such as chute score.

Genetic variability of docility

Independently of the methodology to assess docility, a variety of authors have documented that docility is influenced by several factors such as sex, age, breed, and production system (Cooke, 2011; Haskell et al., 2014; Norris et al., 2014). Regardless of the method used to measure docility, it has been well documented that docility will respond favorably to selection.

For all measures of docility, direct heritability estimates in the literature have a considerable range from 0.03 to 0.67, showing that this trait is heritable (Hearnshaw and Morris, 1984; Fordyce et al., 1982; Haskell et al., 2014). Beckman et al. (2007), reported heritabilities from 0.29 to 0.34 using univariate linear models of standardized scores instead of raw chute scores in Limousin cattle. For this trait Hearnshaw and Morris (1984), reported heritability estimates of 0.03±0.28 for *Bos taurus* calves (sired by Hereford, Simmental and Friesian bulls) and 0.46±0.37 for *Bos indicus*-sired calves (Brahman, Braford and Africander bulls). Burrow (2001) estimated moderate heritabilities for flight speed score ranging from 0.40 to 0.44 in a tropically adapted composite breed of cattle grazed on pasture in the tropics. Here, flight speed score was defined as the time, in hundredths of a second, taken for an animal to cover 1.7 meters after leaving a weighing crush (Burrow et al., 1988). Kadel et al. (2006) estimated heritabilities for flight speed or flight time measured post-weaning and at the start of finishing as 0.30±0.02 and 0.34±0.03, respectively, in Brahman, Belmont Red, and Santa Gertrudis heifers and steers. These authors also reported moderate genetic correlations between flight time and chute score measured at post-weaning and at the start of finishing of -0.37 and -0.35, respectively. A similar genetic correlation estimate was reported by Burrow and Corbet (2000) between flight time and crush score (chute score) of -0.44. These studies suggest that crush score could be used as an indirect measure of the objective measure of flight time. In general, direct heritability estimates in the literature for flight time range from 0.11 to 0.54 (Burrow et al., 1988; Hoppe et al., 2010; Haskell et al., 2014).

A moderate direct heritability estimate of 0.22 for docility tests in Limousin cattle was reported by Le Neindre et al. (1995). However, for docility score several authors have published heritability values with an unweighted mean of 0.26 and a range from 0.0 to 0.61 (Haskell et al., 2014). According to Haskell et al. (2014), irrespective of the model used heritabilities are generally higher for *Bos indicus* and crosses than for *Bos taurus* breeds, perhaps because temperament is generally poorer in *Bos indicus* breeds than *Bos taurus* animals .

Hoppe et al. (2010) estimated genetic correlations between chute score and flight speed ranging between 0.57 and 0.98 in different beef cattle breeds, and more recently Sant'Anna et al. (2013) reported strong genetic correlation estimates between temperament score, crush score, and flight speed, ranging from 0.76 to 0.99. Both studies suggest that a large proportion of the genes underlying one measure of docility also underlie other measures of docility. Similarly, results from Kadel et al. (2006) suggest that the ranking of animals based on genetic predisposition for temperament is consistent over time. To the contrary, disagreement between measures of docility have been reported and are largely confined to differences between objective and subjective measures of flight speed. For instance, Burrow and Corbet (2000) reported moderate (0.45) genetic correlations and low (0.02) phenotypic correlations between the subjective and objectives measures of flight speed scores, suggesting that the observers of flight speed could not adequately differentiate animals using a 1-5 scale to report flight speed. This could be due to the inability to discriminate scores, particularly those that are intermediate.

Some assessments of docility in beef cattle are recommended to be taken at weaning (e.g. chute score), avoiding changes in animal behavior by past experiences (Randel et al., 2012). With any trait measured at weaning, there is the potential that both maternal genetic and maternal permanent environmental effects could play a substantial role in explaining the phenotypic variation of the trait. Burro (2001) estimated a maternal genetic heritability for flight speed scores of 0.05. This was in agreement with the results from several other authors suggesting that the maternal components for docility are low (Prayaga and Henshall, 2005; Beckman et al., 2007).

Models used to analyze docility

Some assessments of docility include subjective scores measured where there is a discrete phenotypic distribution (e.g. chute score, pen score, docility tests, etc.). Some authors have analyzed these traits using linear models instead of threshold models (e.g., Hoppe et al., 2010). However, the theoretically preferred method might be to analyze these discrete traits using threshold models, because it is assumed that the underlying scale of the categorical variable presents a continuous, normal distribution (Quaas et al. 1988; Gianola, 1982). When discrete phenotypic distributions are analyzed with linear models, it is possible that assumptions such as normality and homoscedasticity of residuals would not be met given the discrete nature of the trait and their asymmetric distribution, which means that methods to analyze these variables as a continuous trait would not be appropriate (Gianola, 1982; Lucena et al., 2015). However, Lucena et al., (2015) estimated genetic parameters for temperament in Nellore cattle using both linear ($h^2 = 0.21$) and threshold models ($h^2 = 0.26$) and reported that model choice had little influence on the ranking of animals based on the rank correlations estimates of the EBVs (rank correlations ≥ 0.9). In addition to this, Meijering and Gianola (1985) did not find tangible differences between a linear and threshold model when the number of categories was four or greater, as is the case for most of the scores used to assess docility in beef cattle. Beckman et al. (2007) transformed docility scores to expected normal scores, correcting the scores for inadequacies due to the subjective score system, and after this correction they analyzed docility scores as a linear trait. Although threshold models represent the theoretically appealing model choice to analyze categorical traits because they are based on the assumption that the distribution of a categorical variable is related to an underlying continuous scale (Sant'Anna et al., 2015), linear models may be sufficient to reduce computational complexity, especially in multi-trait analysis involving docility.

Associations of temperament measures with economically relevant traits

Some authors have documented the potential genetic relationship between docility and economically relevant traits. Genetic correlations were reported by Sant'Anna et al. (2013) for weaning weight and flight speed, weaning weight and temperament score, weaning weight and crush score, and between weaning weight and movement score of -0.08 ± 0.07, -0.19 ± 0.07, -0.15 ± 0.09 and -0.01 ± 0.08, respectively. In agreement with Sant't Annta et al. (2013), Burrow et al. (2001) did not find genetic associations between weaning weight and flight speed score (r_g=0.00) or between yearling weight and flight speed score (r_g=0.01) in a tropically adapted composite breed of cattle. Similarly, Prayaga and Henshall (2005) did not find significant genetic correlations between flight times and weaning weight or yearling weight in tropical beef cattle populations. Additionally, Phocas et al. (2006) estimated genetic correlations close to zero between yearling weight and docility score (0.08 ± 0.09) in Limousin heifers. However, Figueiredo et al. (2009) reported one positive and favorable genetic correlation (0.36) between flight distance score and weaning weight in Nellore cattle. These authors agree that selection for docile animals should manifest in modest improvements in weaning weights.

In general, results suggest the existence of low and favorable genetic correlations between temperament and weaning or yearling weights, suggesting that individuals with more desirable temperament could have slightly improved performance (Figueiredo et al., 2009; Hoppe et al., 2010; Sant'tAnna et al., 2012). Following the same trend, phenotypic correlations with temperament traits, generally, are low for weights from birth to one year of age in beef cattle (Haskell et al., 2014). For instance, Burrow (2001), reported negative and close to zero phenotypic correlations between flight speed with birth weight, flight speed with weaning weight, and flight speed with yearling weight of -0.03, -0.02, and -0.05, respectively. Prayaga and Henshall (2005), reported phenotypic correlations of -0.03 and -0.01 for flight time with birth weight and flight time with weaning weight, respectively.

Genetic relationships between growth rate or daily gain suggest that cattle with calmer temperament have greater average daily gain (Burrow, 1997; Voisinet et al., 1997a; Petherick et al. 2002; Hoppe et al., 2010; Sant'Anna et al., 2012), and better scores for conformation, finishing precocity and muscling (Sant'Anna et al., 2015). Similarly, cattle with poor temperament had lower feed intake and spent less time eating (Café et al., 2011a), lower average daily gain, poorer average daily intake and poorer feed conversion efficiency (Petherick et al., 2002; Café et al., 2011a), and lighter carcass weight (Nkrumah et al., 2007; Café et al., 2011a).

Scrotal circumference is commonly used as selection criterion because it has been associated with increased fertility, in males and females, and weights at different ages (Boligon et al., 2011). Some authors have documented genetic and phenotypic correlations between temperament (measured as flight speed or temperament score) with scrotal circumference, suggesting that selection for larger scrotal circumference would not lead to a favorable correlated response with better temperaments (Burrow, 2001; Barrozo et al. 2012; Sant'Anna et al., 2012).

Few authors have quantified the potential genetic relationship between docility and intramuscular fat percentage as a measure of meat quality. Reverter et al. (2003) estimated a negative and close to zero genetic correlation between intramuscular fat and flight time (-0.05) in tropically adapted cattle breeds. Results from Kadel et al. (2006) suggested that improved temperament, evaluated using crush score and flight speed, was genetically correlated with improved tenderness in tropically adapted breeds of beef cattle. Shear force, a measure of tenderness, has been genetically associated with temperament by several authors, with the general consensus that more excitable cattle are prone to produce tougher beef and a higher incidence of dark cutters (Voisinet et al., 1997b; Reverter et al. 2003; King et al., 2006; Café et al., 2011; Hall et al., 2011).

Docility in National Cattle Evaluations

In general, it is expected that calmer beef cattle grow faster with better feed conversion rates (Haskell et al., 2014). However, many production practices such as weaning, ear tagging, vaccinations, transportation, etc., result in added stress, which negatively affect the management and production, and increase the risk of injury for both the handler and the animal (Burdick et al., 2010; Burrow, 1997). Regardless of the method used to measure docility, direct heritability estimates published for docility in beef cattle have been shown to be moderate, which means that if genetic selection for more docile cattle is practiced, change can be made. Consequently, some breed associations are using a subjective measure proposed by the Beef Improvement Federation (BIF; Beef Improvement Federation, 2010). The Beef Improvement Federation guidelines include a method named as "docility score" which is designed to evaluate temperament when cattle are processed in a squeeze chute, and as stated by Randel et al. (2012), many refer to this method as "chute score". According to Randel et al. (2012), most of the breed associations are using the 1 to 6 scoring system proposed by the BIF (Beef Improvement Federation, 2010), and only few of them, for example Brahman and Saler, are using docility or pen scoring systems recorded from 1 to 5. BIF guidelines (Beef Improvement Federation, 2010) suggest to score temperament at weaning or yearling ages, because an animal's behavior can be influenced by past experiences. For this reason, breed associations are recording docility scores at weaning, yearling, or both periods (Randel et al., 2012). The breed associations that assess docility or temperament scores include Angus, Brangus, Simmental, Limousin, Brahman, and Saler (Randel et al., 2012; Beckman et al., 2007; Norris et al., 2014).

Summary

Docility is an important trait in beef cattle which can impact human safety and productivity, animal performance, and meat quality. Several methods have been documented to assess temperament, and although several authors worldwide have reported associations between temperament traits and economically relevant traits. Still there is not a general consensus relative to the genetic correlations between docility and other traits, because results could vary due to several different factors including the type of docility test and the population (breed). Regardless of the method used to measure this trait, direct heritability estimates have shown it to be moderately heritable, meaning genetic progress can be made in the pursuit of calmer temperament. It is expected that selection in beef cattle to improve docility will have positive benefits relative to herd management via cattle that respond in a more favorable fashion, decreased injury of both animals and handlers, and improved animal performance resulting in increased profit for cattle producers. For this reason, several breed associations are including docility in their genetic evaluations.

Genetic parameters for docility, weaning weight, yearling weight and intramuscular fat percentage in Hereford cattle

Abstract

Cattle behavior, including measures of docility, is important to beef cattle producers not only from a human safety perspective, but also due to potential correlations to economically relevant traits. Field data from the American Hereford Association was used to estimate genetic parameters for chute score (CS; n=25,037), weaning weight (WW; n = 23,908), yearling weight (YW; n=23,978) and intramuscular fat percentage (IMF; n = 12,566). Single-trait and bivariate animal models were used to estimate heritabilities and genetic correlations. All models included fixed effects of sex and contemporary group, defined as herd-year-season, and included direct genetic and residual components as random effects. For CS and WW, additional random effects of maternal genetic and maternal permanent environment were also fitted. For CS, WW, YW, and IMF, heritability estimates were 0.27±0.02, 0.35±0.03, 0.36±0.02, and 0.27±0.02, respectively. Genetic correlations between CS and WW, CS and YW, CS and IMF, WW and YW, WW and IMF and YW and IMF were -0.12±0.06, -0.10±0.05, -0.08±0.06, 0.47±0.05, -0.19±0.09, and -0.41±0.05, respectively. Heritability estimates for all traits suggest that they would respond favorably to selection, and selection for increased WW or YW could decrease marbling. Genetic correlations between CS and WW, YW, and IMF were all favorable but weak, suggesting that selection for improved docility will not have negative consequences on growth or carcass quality. Furthermore, maternal additive and maternal permanent

environmental variances for CS were near zero, suggesting that their inclusion in Nation Cattle Evaluation is not warranted.

Key words: Beef cattle, genetic parameters, docility, intramuscular fat percentage.

Introduction

It is well documented that cattle vary in their response to stressors and environmental changes. In fact, overly aggressive animals are considered as undesirable given potential safety risks to human handlers (Cafe et al., 2011b; Turner et al., 2011). Conversely, calm temperament has been associated with increased ADG, health, meat quality and superior responses to infections, which improves overall herd productivity (Burrow, 1997; Fell et al., 1999; Kadel et al., 2006). Moreover, temperament traits are important because feedlot managers and producers suggest that excitable cattle could be more costly to raise in terms of required handling time, labor, and equipment repair (Hall et al., 2011). Due to the associations between temperament and production traits, assessment of beef cattle temperament has increased in recent years (Norris et al., 2014). Consequently, several breed associations are now routinely measuring docility to include in national cattle evaluations (Beckman et al., 2007; Norris et al., 2014). The phenotype that is currently used in National Cattle Evaluations is the subjective (due to the perception of the observer) measure of chute score (Beef Improvement Federation, 2010).

Despite the attention that quantifying temperament has received, there is not a general consensus relative to the genetic correlations between docility and economically relevant traits, because results could vary due to several different factors (e.g., method of evaluating docility, rearing conditions, breeds, etc.; Haskell et al., 2014; Norris et al., 2014). Before a docility selection metric can be added to a genetic evaluation, any potential antagonisms with economically relevant traits or indicator traits should be quantified. Consequently, the objective of the current study was to estimate genetic parameters for chute score, weaning weight, yearling weight, and intramuscular fat percentage in Hereford cattle.

Materials and methods

Animal Care

Data were provided by the American Hereford Association (AHA) and, therefore, the project was not subject to animal care and use committee approval.

Data

Initial data from 130,263 animals, born between 1979 and 2014, were supplied by the AHA (Kansas City, MO). Animal records included 205-d weight adjusted for calf and dam age (weaning weight [WW]), age adjusted yearling weight (YW), chute score (CS) and age adjusted intramuscular fat percentage (IMF) measured via ultrasound following Beef Improvement Federation guidelines (Beef Improvement Federation, 2010). Data were edited such that animals without sire or dam information were removed. Contemporary groups (CG) of less than 10 animals or without variation in CS scores were removed. For YW, animals from CG with less than 10 animals were removed. For IMF, records from CG with less than 10 animals were considered as missing values. Records from 25,037 animals weaned between 2010 and 2014, with YW from 2011 and 2015 were retained. The final pedigree file included 172,867 animals, with 9,079 sires and 62,272 dams.

Chute scores were obtained at weaning, following the method proposed by Grandin (1993), and following the scoring system recommended by the Guidelines for Uniform Beef Improvement Programs (Beef Improvement Federation, 2010) in which high scores reflect poor docility. According to this classification, animals with scores of 1 are considered docile or calm, a score of 2 indicates animals that are restless or shifting, a score of 3 indicates animals that are squirming or nervous, a score of 4 indicates animals that are flighty (wild), and scores 5 and 6 represent aggressive and very aggressive animals, respectively (Grandin, 1993; Beef Improvement Federation, 2010). The final data file included 25,037 records for CS, 24,908 records for WW, 23,978 records for YW, and 12,566 records for IMF. The descriptive information of WW, YW, CS, and IMF are presented in Table 1. Chute score was characterized by a skewed distribution as a consequence of a greater number of observations for score 1 (n = 20,495; representing 81.86% of the total observations) compared with score 2 (n = 3,646), score 3 (n = 728), score 4 (n = 143), score 5 (n = 23), and score 6 (n = 2).

For each trait, 2 weaning seasons were defined: January through June and July through December. Contemporary groups (CG) for each trait were formed by the combination of herd-year-season.

Statistical analyses

In the current study, CS was treated as a linear trait. Six bivariate linear-linear animal models were fitted to estimate (co)variance components between traits, and starting values for each trait were initially estimated with similar single-trait animal models using ASReml software (Gilmour et al., 2009). Final models included the fixed effects of sex and CG. Direct additive genetic and residual effects were included as random effects. For CS and WW, maternal genetic and maternal permanent environmental components were also fitted as random effects.

In matrix notation, the model for YW, and IMF can be represented as:

$$\boldsymbol{Y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{e} \qquad [1]$$

When CS and WW were analyzed, the model can be represented as:

$$\boldsymbol{Y} = \boldsymbol{Xb} + \boldsymbol{Z_1a} + \boldsymbol{Z_2m} + \boldsymbol{Z_3p} + \boldsymbol{e} \qquad [2]$$

Where in which Y represents the vector of records for the traits; b is the vector of fixed effects; a is the vector of random additive genetic effects of the animals; m is the vector of random maternal genetic effects of the dams; p is the vector of maternal permanent environment effects of the dams; e is an unknown vector of random environmental effects; X, Z, Z1, Z2, and Z3 are incidence matrices relating observations to fixed, animal (model 1), animal, maternal, and maternal permanent environmental effects (model 2), respectively.

For model 2, the expectations and (co)variance matrices for random effects are described as:

$$\mathbf{E}\begin{bmatrix}\mathbf{Y}\\ \mathbf{a}\\ \mathbf{m}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{Xb}\\ \mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix};\quad \mathbf{V}\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G_a} & \mathbf{G_{am}} & \mathbf{0} & \mathbf{0}\\ \mathbf{G_{am}} & \mathbf{G_m} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{P} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\otimes\mathbf{G_a} & \mathbf{A}\otimes\mathbf{G_{am}} & \mathbf{0} & \mathbf{0}\\ \mathbf{A}\otimes\mathbf{G_{am}} & \mathbf{A}\otimes\mathbf{G_m} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I_D}\otimes\mathbf{P} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I_O}\otimes\mathbf{R}\end{bmatrix},$$

in which $\mathbf{G_a}$, $\mathbf{G_m}$, $\mathbf{P}$ and $\mathbf{R}$ denote the matrices containing additive genetic, maternal genetic, maternal permanent environmental, and residual (co)variance components, respectively; $\mathbf{G_{am}}$ represents the direct-maternal additive genetic covariance; $\mathbf{A}$ is the numerator relationship matrix; $\mathbf{I_D}$ is an identity matrix accounting for the number of dams with offspring; and $\mathbf{I_O}$ is an identity matrix for the total number of observations.

Results and discussion

Heritability estimates using single-trait models are presented in Table 2. Direct heritability estimates were 0.36 ± 0.02, 0.35 ± 0.03, 0.27 ± 0.02, and 0.27 ± 0.02 for YW, WW, CS, and IMF, respectively. (Co) variance estimates can be found in Table 3 and heritability, genetic, and residual correlation estimates can be found in Table 4. For CS, all bivariate models included only direct effects as maternal components estimated from the univariate analysis were near 0.

Norris et al. (2014) stated that among all methods documented to assess temperament or docility in cattle, the most common methods used are CS, pen score, and exit velocity. Regardless of the method used to measure docility, direct heritability estimates in the literature have a considerable range (from 0.03 to 0.67; Fordyce et al., 1982; Hearnshaw and Morris, 1984; Haskell et al., 2014). The direct heritability estimate of 0.27 (0.02) reported from the current study is similar to the range of estimates (0.29 to 0.34) reported by Beckman et al. (2007), who used a univariate linear animal model using standardized scores instead of raw CS. Flight speed (FS), the velocity at which the animal leaves a restraining device, has been studied by several authors (e.g., Burrow, 1997; Haskell et al., 2014). The CS heritability estimate estimated herein (0.27 ± 0.02), using a single-trait animal model, was similar to the estimate of 0.28 (0.05) for FS reported by Sant'Anna et al. (2015). Hoppe et al. (2010) estimated genetic correlations between CS and FS ranging between 0.57 and 0.98 in different beef cattle breeds, and more recently, Sant'Anna et al. (2013) reported strong genetic correlation estimates between temperament score, crush score, and FS, ranging from 0.76 to 0.99. Both studies suggest that a large portion of the genes underlying one measure of docility also underlie other measures of docility. Similarly, results from Kadel et al. (2006) suggest that the ranking of animals based on genetic predisposition for temperament is consistent over time, where the average age at the first and second recordings was 246 and 564 days. These authors reported genetic correlations ranging from 0.98 and 0.96 for flight time and crush score measured over time. To the contrary, disagreements between measures of docility have been reported and are largely confined to differences between objective and subjective measures of FS. For example, Burrow and Corbet (2000) reported moderate (0.45) genetic correlations and low (0.02) phenotypic correlations between the subjective and objectives measures of FS scores, suggesting that the observers of FS could not adequately differentiate animals using a 1 to 5 scale to report FS. This could be due to the inability to discriminate scores, particularly those that are intermediate. However, the same authors reported genetic and phenotypic correlations between objective FS and subjective crush score of –0.45 and –0.44, respectively, suggesting that relative to subjective measurements of temperament, crush score is more desirable than a subjective measure of FS.

Among U.S. beef cattle breed associations that provide a selection tool to improve docility, some breed associations suggest scoring docility at yearling age and others at weaning. The benefit of scoring docility at weaning is the ability to garner CS information on more animals (larger CG) before selection for other traits (e.g., growth) occurs. However, for any trait measured at weaning, there is the potential that both maternal genetic and maternal permanent environmental effects could play a substantial role in explaining the phenotypic variation of the trait. In the current study, estimates of both maternal genetic and maternal permanent environmental components for CS were near 0. This is in agreement with the results from several other authors suggesting that the maternal components for docility are low (Burrow, 2001; Prayaga and Henshall, 2005; Beckman et al., 2007) and that the inclusion of these effects in genetic evaluations for CS is not warranted.

In the current study, direct heritability estimates for WW ranged from 0.23 to 0.35, with smaller maternal heritability estimates ranging from 0.12 to 0.15. The direct heritability estimates for WW with CS and WW with YW followed the same pattern as the estimates using a single-trait model (0.35 ± 0.03 and 0.32 ± 0.03, respectively); however, the estimate for WW with IMF was lower (0.23 ± 0.03). A similar pattern was observed for maternal heritability estimates for WW with CS and WW with YW (0.15 ± 0.02) and for WW with IMF (0.12 ± 0.03). The lower heritability (direct and maternal) estimates for WW when fitted in a bivariate model with IMF are due to the fact that a reduced subset of animals was used such that all animals had both traits recorded. This was done because a comparatively large number of WW CG did not have IMF observations. The direct heritability estimates were within the range of literature values, 0.07 to 0.57, reported by other authors (Schoeman and Jordaan, 1999; Plasse et al., 2002). Maternal heritability estimates for WW in the literature vary from 0.06 to 0.21 (Haile-Mariam and Kassa-Mersa, 1995; Diop and Van Vleck, 1998). The maternal heritability estimates for WW from the current study (0.15 ± 0.02) were slightly lower than the weighted mean of 0.18 published by Koots et al. (1994). In the current study, a negative and significantly different from 0 direct-maternal covariance was estimated for WW. Both positive and negative estimates have been reported in the literature; however, the majority of estimates tend to be negative

(Meyer, 1992; Schoeman and Jordaan, 1999; Speidel et al., 2007). Heritability estimates for YW ranged from 0.35 to 0.36 with small SE (from 0.02 to 0.03), which is within the range of estimated values in different beef cattle populations (e.g., Meyer, 1992; Mohiuddin, 1993).

Using 2-trait animal models, the heritability estimate for IMF was identical (0.27 ± 0.02) to the estimate using a single-trait model. The direct heritability for IMF estimate in this study was similar to the estimate from MacNeil et al. (2010) using Angus field data (0.31 ± 0.03) and to the estimates of 0.18, 0.30, and 0.25 for bulls, heifers, and steers, respectively, previously reported by MacNeil and Northcutt (2008). The estimate from the current study is slightly lower than the estimate of 0.41 reported by Bertrand et al. (2001) and the more recent estimate of 0.38 reported by Mateescu et al. (2015) in Angus cattle. Estimates of genetic and environmental correlations among traits are presented in Table 4. Only the genetic correlation between YW and WW was moderate and positive. The rest of the genetic correlation estimates were negative, with a range from –0.41 to –0.08. The negative genetic correlation estimate between YW and IMF was the strongest (–0.41 ± 0.05) followed by IMF with WW (–0.19 ± 0.09). The lowest genetic correlation estimates in magnitude were between CS and WW, CS and YW, and CS and IMF, with values of –0.12 ± 0.06, –0.10 ± 0.05, and –0.08 ± 0.06, respectively. The highest residual correlations were between YW and WW (0.31 ± 0.02) and between YW and IMF (–0.48 ± 0.02). Residual correlations among all the other traits were close to 0, with a range from –0.04 to 0.05, with relatively large SE of 0.02. The positive genetic correlation between WW and YW is in agreement with other published estimates (Koots and Gibson, 1996). Of specific interest in the current study were the genetic correlations between CS and WW, YW, and

IMF. The genetic correlation between CS and WW was low and negative –0.12 ± 0.06, indicating that selection for higher WW would result in selecting animals with calmer temperament. Similar genetic correlations have been reported by Sant'Anna et al. (2013) for WW and FS (–0.08 ± 0.07), WW and temperament score (–0.19 ± 0.07), WW and crush score (–0.15 ± 0.09), and WW and movement score (–0.01 ± 0.08). Figueiredo et al. (2009) reported positive and favorable genetic correlations (0.36) between flight distance score and WW in Nellore cattle, where 1 refers to very reactive animals and 5 refers to very docile animals. These authors agree that selection for docile animals should manifest in modest improvements in WW. However, Burrow (2001) did not find genetic associations between WW and FS score (genetic correlation, r_g = 0.00) or between YW and FS score (r_g = 0.01) in a tropically adapted composite breed of cattle. In agreement with Burrow (2001), Prayaga and Henshall (2005) did not find significant genetic correlations between flight times and WW or YW in tropical beef cattle populations. Additionally, Phocas et al. (2006) estimated genetic correlations close to 0 between YW and docility score (0.08 ± 0.09) in Limousin heifers. Results suggest the existence of low and favorable genetic correlations between temperament and WW or YW, suggesting that individuals with more desirable temperament could have slightly improved performance (Figueiredo et al., 2009; Hoppe et al., 2010; Sant'Anna et al., 2012). The underlying physiological explanation for these associations is not well documented in intensive systems (Sant'Anna et al., 2015). Plasma cortisol and other metabolite concentrations, mainly glucose and lactate, have been significantly associated with poor temperament (Cafe et al., 2011a). Cafe et al. (2011a) suggested that more excitable animals show greater activation of the hypothalamic–pituitary–adrenal axis resulting in the production of more cortisol and glucose, and several authors have found that lower levels of cortisol are associated with higher growth rates (Purchas et al., 1980).

Few authors have quantified the potential genetic relationship between docility and IMF as a measure of meat quality. The genetic correlation between IMF and CS from the current study (–0.08 ± 0.06) was similar to that observed by Reverter et al. (2003), who estimated a negative and close to 0 genetic correlation between IMF and flight time (–0.05) in tropically adapted cattle breeds. Results from Kadel et al. (2006) suggested that improved temperament, evaluated using crush score and FS, was genetically correlated with improved tenderness in tropically adapted breeds of beef cattle. Shear force, a measure of tenderness, has been genetically associated with temperament by several authors, with the general consensus that more excitable cattle are prone to produce tougher beef and a higher incidence of dark cutters (Voisinet et al., 1997; King et al., 2006; Hall et al., 2011). Although the influence of IMF on beef palatability has been controversial, the visual appearance due to marbling is often associated with favorable meat quality and certainly plays an important role in purchasing decisions and price (Chambaz et al., 2003). The results from the current study suggest that marbling should not be negatively impacted by long-term selection for CS and could be slightly improved. Admittedly, the genetic correlations estimated herein are confined to a population whereby the majority of cattle were considered to be calm. In populations where a greater proportion of animals were considered aggressive, the genetic correlations between CS and IMF could be greater.

In conclusion, heritability estimates from the current study suggest that CS would respond favorably to selection and improvement in this trait could be made. For CS, the maternal component did not explain any of the phenotypic variation, suggesting that inclusion of a maternal effects model is not warranted for CS. Although favorable associations were found between docility and WW, YW, and IMF, the SE were relatively large.

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Tables

Table 1. Descriptive statistics for chute score, weaning weight, yearling weight and intramuscular fat percentage

Trait	No.	Mean	Min[1]	Max[2]	SD	CV, %
Chute Score	25,037	1.22	1	6	0.53	43.2
Weaning Weight, kg	24,908	264.6	85.4	469.7	42.5	16.1
Yearling Weight, kg	23,978	414.1	147.7	743.9	80.4	19.4
Intramuscular Fat, %	12,556	3.2	0.6	9.6	1.0	32.6

[1]Min is the minimum value.

[2]Max is the maximum value.

Table 2. Variance component and heritability estimates (SE) using single-trait models for chute score, weaning weight, yearling weight and intramuscular fat percentage

Parameter[1]	Chute score	Weaning weight, kg	Yearling weight, kg	Intramuscular fat, %
σ^2_a	0.056 (0.004)	327.9 (29.5)	2,076.2 (127.0)	0.26 (0.02)
σ^2_m	0.000 (0.000)	141.1 (21.8)	-	-
$\sigma_{a\text{-}m}$	0.000 (0.000)	-124.5 (22.0)	-	-
C^2	0.008 (0.002)	130.8 (12.8)	-	-
σ^2_e	0.145 (0.003)	449.5 (17.9)	3,685.9 (97.6)	0.72 (0.02)
σ^2_p	0.208 (0.002)	924.7 (10.4)	5,762.1 (62.2)	0.98 (0.01)
h^2_a	0.27 (0.02)	0.35 (0.03)	0.36 (0.02)	0.27 (0.02)
h^2_m	0.00 (0.00)	0.15 (0.02)	-	-
r_{am}	0.00 (0.00)	-0.58 (0.06)	-	-

[1]σ^2_a= additive genetic variance; σ^2_m= maternal genetic variance; $\sigma_{a\text{-}m}$= direct-maternal genetic covariance; C^2= maternal permanent environmental variance; σ^2_e= residual variance; σ^2_p= phenotypic variance; h^2_a= additive heritability; h^2_m= maternal

heritability; and r_{am}= direct-maternal correlation. **Table 3.** (Co)variance component estimates (SE) using 2-trait models for chute score, weaning weight, yearling weight, and intramuscular fat percentage

	Trait 1 – Trait 2[2]					
Parameter[1]	CS – WW	CS – YW	CS – IMF	YW - WW	IMF - WW	YW – IMF
$\sigma^2_{a,1}$	0.061 (0.004)	0.060 (0.004)	0.054 (0.005)	2,017.4 (121.2)	0.26 (0.02)	1,413.2 (123.1)
$\sigma^2_{e,1}$	0.149 (0.003)	0.149 (0.003)	0.131 (0.004)	3,733.5 (94.1)	0.71 (0.02)	2,938.9 (98.5)
$\sigma^2_{a,2}$	326.8 (29.4)	2,073.5 (126.9)	0.26 (0.02)	293.0 (26.9)	183.3 (26.6)	0.26 (0.02)
$\sigma_{a\text{-}m,2}$	-123.3 (21.9)	-	-	-84.8 (18.6)	-63.2 (21.5)	-
$\sigma^2_{m,2}$	140.1 (21.7)	-	-	140.7 (18.7)	99.1 (23.4)	-
$\sigma^2_{e,2}$	450.6 (17.9)	3,687.8 (97.6)	0.72 (0.02)	479.0 (16.8)	475.0 (18.7)	0.72 (0.02)
$C^2_{,2}$	130.0 (12.7)	-	-	98.6 (10.6)	107.0 (16.0)	-

[1] σ^2_a= additive genetic variance; σ^2_m= maternal genetic variance; $\sigma_{a\text{-}m}$= direct-maternal genetic covariance; C^2= maternal permanent environmental variance; and σ^2_e= residual variance. Parameter 1 and parameter 2 relate to trait 1 and 2, respectively.

[2] CS=chute score; WW= weaning weight (kg); YW= yearling weight (kg); and IMF= intramuscular fat percentage.

Table 4. Estimates of heritabilities (on diagonal), genetic correlations (above diagonal) and environment correlations (below diagonal) with their standard errors (SE) from bivariate models for chute score, weaning weight, yearling weight and intramuscular fat percentage.

Trait[1]	CS	WW_d	WW_m	YW	IMF
CS	0.29 (0.02)	-0.12 (0.06)	0.02 (0.07)	-0.10 (0.05)	-0.08 (0.06)
WW_d	-0.04 (0.02)	0.23 to 0.35 (0.03)	-0.58 to -0.47 (0.06 to 0.11)	0.47 (0.05)	-0.19 (0.09)
WW_m	-	-	0.12 to 0.15 (0.02 to 0.03)	0.46 (0.07)	0.23 (0.10)
YW	-0.04 (0.02)	0.31 (0.02)	-	0.32 to 0.36 (0.02 to 0.03)	-0.41 (0.05)
IMF	0.02 (0.02)	0.05 (0.02)	-	-0.48 (0.02)	0.27 (0.02)

[1]CS = chute score; WW_d= direct genetic component for weaning weight; WW_m= maternal genetic component for weaning weight; YW = yearling weight; and IMF= intramuscular fat percentage.