DISSERTATION

DEVELOPMENT OF A MULTI-BREED HEIFER PREGNANCY GENETIC EVALUATION IN BEEF CATTLE

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ABSTRACT

DEVELOPMENT OF A MULTI-BREED HEIFER PREGNANCY GENETIC EVALUATION IN BEEF CATTLE

Heifer fertility represents a primary influence on the profitability of a beef cow-calf enterprise. Reproductive rates determine the number of calves born and thus influence the amount of beef product produced at the commercial level driving income for cow-calf operators. Heifer fertility then is an economically relevant trait, though in most cases pregnancy data are cumbersome, untimely to collect, and are considered a rare phenotype in national cattle evaluations (NCE). Despite this, there are successful examples of existing evaluations for heifer pregnancy (HP) across several beef breed associations. These HP genetic evaluations typically rely on categorical exposure (1 = exposed; 0 = not exposed) and pregnancy outcome (1 = pregnant; 0 = not pregnant) data and involve the use of threshold animal models (TM) to convert these binary observations to an underlying normally distributed range of values known as liabilities. These liabilities are then expressed as a percentage that predicts the likelihood of a bull's daughters becoming pregnant and giving birth as two-year-olds in the form of an expected progeny difference (EPD).

However, despite these existing HP genetic evaluations, little improvement in the genetic trends in HP has been observed. Perhaps the reason for meager improvement in genetic trend is seedstock producers are not placing enough emphasis on HP, or with pregnancy rates already at or near 90% there is an assumption there is no need for genetic improvement. Additionally, though TM have been successfully implemented in genetic evaluations of HP, a common challenge with the methodology is the inability to evaluate data from contemporary groups that all have the same observation. Even more important is that TM are not supported in some software used for single-step genomic evaluation, such as BOLT by Theta Solutions. Because of these challenges, this study investigated the development of a multi-breed genetic

evaluation for HP by performing a series of HP evaluations using TM, linear animal model (LM), and random regression model (RRM) methods. This study used HP data collected on heifers from 1974 to 2020 provided by the International Genetic Solutions (IGS) genetic evaluation, sourced from 9 partner breed associations. Because each breed organization may have its own nuanced definition of HP or differences in how data are reported, inconsistencies in HP data need to be investigated. For example, the American Simmental Association (ASA) does not have an upload format for producers to report HP data but instead uses a system of logic converting whole herd reporting (WHR) codes into HP phenotypes.

The first study described the framework for how the ASA converted productivity, culling, and enrollment codes into HP phenotypes. It then evaluated the relative proportions of reasons why heifers/cows were culled. The proportion of heifers culled due to reproductive failure using this method of establishing HP phenotypes was 14%, which is consistent with the national average. The summary statistics for HP observations were cohesive with other HP observations reported to IGS partner breed organizations. Evaluating the effectiveness of these created phenotypes were investigated in the second study.

Using data from the American Gelbvieh Association, the Red Angus Association of America, the North American Limousin Foundation, the American Shorthorn Association, and the Canadian Limousin Association, the second study estimated variance components, breed effects, and heterosis effects using LM and TM evaluation methods. Evaluations of HP were performed first within breed before a multibreed population was developed. The average heritability estimate across evaluations performed on 7 different breed groups for HP using LM methods was 0.026, with a minimum value of 0 and a maximum of 0.084. The average heritability for HP using TM methods was 0.17, with a minimum of 0.07 and a maximum of 0.28. Breed populations were then combined into a single multi-breed population, and the same stepwise procedure of incorporating heterosis and breed effects as fixed effects was used to generate variance components and fixed effect solutions. The heritability estimates in this multi-breed population were 0.023 and 0.088 using LM and TM methods, respectively. Heritability estimates did not change as additional fixed effects of breed and heterosis were fit. There were no

statistically meaningful breed effects; however, heterosis results in a 17.2% increase ($P<0.05$) in the probability of HP when maximum heterosis is achieved. Results from this statistical method suggested that LM and TM may be performing equivalently for estimating HP breeding values in within-breed populations; however, in a multi-breed population, results were inconsistent, suggesting perhaps the model was over-specified with breed effects. These results suggest that LM as the model type within a genetic evaluation may be an alternative evaluation method for HP due to its simplicity, ability to use all available information, and support in modern genetic evaluation software programs.

Due to being relatively simple to collect and economically important for beef producers, the third study performed a series of evaluations for age at first calving (AFC), which also served as an important investigation as AFC was a potential age covariate in HP evaluations. Models were implemented using single-breed populations and then combined into a larger multi-breed population so heterosis and breed effects could be estimated. The heritability estimates of AFC for Simmental and Red Angus were 0.19 ± 0.01 and 0.14 ± 0.01, respectively. These results demonstrate AFC in days is lowly to moderately heritable. However, when evaluating the genetic trend for both breeds the results seemed incongruous as AFC was sharply increasing over time. Many beef producers mass mate heifers at a single fixed breeding date. As a result, older heifers in a CG will not have the ability to have a younger AFC compared their younger counterparts in the same CG if conception occurs on the same day. To account for this systematic management influence which may be creating a disadvantage in some heifers, age differential (DIFF) was included to account for age differences prior to first exposure and was defined as the difference in days between an individual's birth date and the earliest birth date of an animal in a defined contemporary group. In addition to including DIFF as a fixed effect, accounting for heifer body weight prior to breeding was also considered, and subsequent bivariate animal models of AFC that included yearling weight (YW) were performed. Two bivariate multi-trait animal models for AFC and YW with random additive genetic and residual effects and fixed effects of contemporary group, breed proportion, and retained hybrid vigor were used. When DIFF was not included as a fixed effect, the additive, residual, and phenotypic variances for AFC were 126.1, 456.8, and 582.9 d^2, respectively, and

the genetic correlation between AFC and YW was 0.36 ± 0.02. When DIFF was included as a fixed effect, the additive, residual, and phenotypic variances for AFC were 10.0, 326.0, and 336.0 d^2, respectively. The genetic correlation between AFC and YW was 0.19 ± 0.04. In the absence of DIFF, the heritability estimates for AFC and YW were 0.22 ± 0.01 and 0.44 ± 0.01, respectively, but were 0.03 ± 0.003 and 0.44 ± 0.01 respectively, when DIFF was included. Age differential had a significant effect on AFC at –0.86 ($P < 0.0001$). The low additive genetic variance of AFC, when accounting for DIFF, suggests that the influence of a female's age going into a fixed breeding date explains much of the variation in AFC.

Because of the potential drawbacks associated with LM and TM evaluations of HP, the fourth study investigated alternative definitions of HP using RRM evaluation methods. Two fertility traits evaluated using RRM were proposed; the first being the evaluation of heifer pregnancy by calving week (HPcw), which regresses a binary calving event on the week a heifer calved within her contemporary groups calving window, and the second being the linear evaluation of binary HP which regresses HP on an age covariate such as age at first exposure (AFE) or yearling age (YAGE). In all evaluation methods, Legendre polynomials were used as the base function and observed heritability estimates at different age ranges were transformed from the (co)variances estimated for the intercept and linear term of HPcw or HP. Within the HPcw evaluations, two separate age covariates were proposed as additional fixed effects, with the first being age at first calving (AFC), and the second being AFE. Heritability estimates for HPcw fitting AFC as a fixed effect ranged from 0.39 to 0.56, though this is assuredly from AFC being a biased age estimate. Observed heritability estimates for HPcw across 10 weeks, fitting AFE as a fixed effect ranged from 0.010 to 0.20, which are more realistic and consistent with literature estimates compared to observed HPcw heritability estimates fitting AFC as an age covariate. For the HP evaluation regressing HP on YAGE, heritability estimates ranged from 0.01 to 0.14, suggesting that up to 14% of the variation in HP across ages could be attributed to differences in additive genetics. For the evaluation regressing HP on AFE, heritability estimates were 0 or near zero, so this evaluation method likely requires additional scrutiny. Differences in heifer age covariate and trait definition for the evaluation of HP provided

expanded opportunities for the development of national cattle evaluations using RRM. The potential advantages of utilizing RRM in evaluations of categorical or single observation data are that it allows the use of all available data in a dataset and is more adapted to single-step genomic evaluation software systems. Because of this, RRM may be the preferred evaluation method for HP or related fertility traits, though this requires additional testing in global databases.

Results from previous studies suggest there are options for evaluating HP in a multi-breed NCE, but no single method is ideal. While LM evaluations validate well, there is low variance in the EBV for the populations evaluated due to low heritability. The TM evaluations validate well and have reasonable predictions, but they cannot appropriately utilize all available data and are not supported by some modern genetic evaluation software programs. The potential of RRM evaluation methods is evident; however, further testing of this methodology must be performed before this approach can be considered.

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CHAPTER 1 – INTRODUCTION

Genetic improvement in the beef industry begins at the seedstock level, where a small number of breeders make intensive selection decisions to continually improve the genetic merit of their animals for economically important traits (ERT) in the commercial level (Golden et al., 2000). Commercial cow/calf producers can take advantage of genetic progress made in the seedstock sector by buying parent animals from seedstock breeders to use in their herds, thus improving their own cow herd genetics. Seedstock breeders rely on robust national beef cattle genetic evaluations (NCE) to supply selection tools in the form of expected progeny differences (EPD) and selection indexes to identify genetically superior animals to use in their production systems. Consequently, NCE relies on seedstock breeders to report raw data on phenotypes of interest to support large-scale genetic evaluation of ERT through best linear unbiased prediction (BLUP) methodology. Historically, NCE were limited to single breed populations, and data were funneled to the genetic evaluations through the registry services of a breed association. However, more recent innovations in genetic evaluation methodology have allowed for massive, multi-breed genetic evaluations that can better predict genomically enhanced EPD on animals across multiple breed populations (Golden et al., 2016).

Data for the analyses in this dissertation were provided by International Genetic Solutions (IGS), a genetic evaluation company that services numerous beef breed associations and affiliated industry organizations. As of writing this dissertation, the IGS genetic evaluation calculates EPD and selection indexes for approximately 22 million animals weekly. The EPD produced by IGS currently consist of: calving ease direct, birth weight, weaning weight, post-weaning gain, average daily gain, milk, calving ease maternal, docility, stayability, carcass weight, ribeye area, fat thickness, marbling, and shear force. A notable absence in the suite of IGS EPD is a selection tool for improved heifer fertility. The aim of this dissertation was to investigate the development of a multi-breed NCE of heifer pregnancy (HP) for IGS.

The reasons for development of a multi-breed genetic evaluation for HP are twofold; the first is a multi-breed evaluation produces estimates that are more easily compared across breed populations included in the evaluation. This eliminates the need for across-breed adjustment factors (Kuehn and Thallman, 2022) on EPD and provides a more accessible way for commercial cow/calf producers to identify different breed-type bulls for use in crossbreeding programs to capture added performance through heterosis. The second reason, and perhaps more impactful, is that a multi-breed genetic evaluation can capture greater numbers of progeny records through common sires used in different breed populations (Culbertson, 2021) and improve the accuracy of the predictions. In a report to the American Simmental Association (ASA), sires with progeny registered in multiple other breed populations exceeded 4.5 million calves, where only 2.4 million of their sired calves were registered with the ASA, resulting in a 1.9 increase in progeny data for the common-used sires (Atkins et al., 2023). Presently, there are within-breed examples of NCE for HP being implemented by the Red Angus Association of America (RAAA), the American Gelbvieh Association (AGA), and the American Angus Association (AAA), but a multi-breed genetic evaluation for HP could add a greater amount of data and thus produce higher prediction accuracy.

Heifer fertility is a complex trait with numerous factors influencing successful pregnancy and as such, can be a challenging trait to predict in beef cattle (Wathes et al., 2008; Cammack et al., 2009). While there are potentially a variety of traits that could be used for selection to improve heifer fertility, perhaps the simplest to observe is the binary success/failure approach. This technique utilizes categorical values (1 = pregnant; 0 = not pregnant) to assign success or failure of pregnancy observed on a contemporary group of heifers that were first given the opportunity to become pregnant. Categorical, non-linear variables can be challenging to model in BLUP evaluations (Fernando et al., 1983) and since categorical values are not normally distributed, the variance of a categorical trait is a function of its expectation and often results in heterogeneity of variance in linear models (Gianola, 1982). A solution to this problem is to evaluate the underlying continuous unobservable trait measured with a categorical variable where the underlying variable is normally distributed and often referred to as a liability (Falconer

and McKay, 1996). The observed categorical responses are determined by whether an animal exceeds a particular threshold, and hence, is why these models are typically referred to as threshold models (Mrode, 2014).

The liability is not an observable phenotype but determine the observable phenotype. As such, threshold models use a non-linear system of equations to generate solutions for animal random genetic effects from mixed model equations via an iterative method (Gianola and Foulley, 1983). Historically, this iterative method meant threshold models were more complex and required greater computational requirements which led to more costly genetic evaluations (Misztal et al., 1989; Mrode, 2014). However, innovations in computing power and genetic evaluation methods have effectively eliminated any cost differences of threshold models compared to linear models (Campos et al., 2019; Nayeri et al., 2019). Perhaps the more pressing issue with threshold models is when all responses for a given class of a factor occur (e.g. all heifers are pregnant in a contemporary group) this results in an extreme category, commonly referred to as the Extreme Category Problem (ECP). When an ECP occurs in a threshold model the solutions to such classes tend to $\pm \infty$ or 0 as the iterations proceed, resulting in poor or lack of convergence (Misztal et al., 1989). To overcome this, Harville and Mae (1984) suggested treating the fixed factors as random or eliminating the observations causing the problem – though neither solution is ideal. The first solution is restrictive and violates the assumptions required of a threshold model, and the second solution dictates using different data for different models which would distort the inferences and not be representative of the entire population and therefore may not be appropriate for NCE (Misztal et al., 1989).

Despite these challenges, the ability of a threshold model to more effectively evaluate non-linear data was shown in a simulation study using binary data, where Meijering and Gianola (1985) demonstrated that a threshold model produced breeding values that were more similar to the true breeding values compared with a linear model. As the incidence of a binary trait and its heritability decreases, a threshold model was more effective, thus making threshold models the method of choice for lowly-heritable binary traits (Meijering and Gianola, 1985; Mrode, 2014; Gianola and Rosa, 2015).

Traditional HP genetic evaluations use threshold models to estimate the probability that a sire's daughters will be more or less likely to become pregnant at a year of age. These evaluations can be restrictive, limiting the use of only same-breed records and of records to only specific points in the life of an animal (Speidel and Enns, 2015) often resulting in lower accuracy breeding values compared to those obtained through genetic evaluations using linear models. And while genomic information can provide an avenue for improved accuracy of genetic prediction, threshold models are not readily adaptable to the incorporation of genomic information through single-step methods other than genomic relationship matrices (Legarra et al., 2009; Speidel et al., 2018).

Inversion of genomic relationship matrices present computational restrictions when many genotyped animals are present in a population as seen in many breed populations today such as the American Angus Association with over 1 million genotypes, and over 600,000 genotypes in the IGS multi-breed genetic evaluation. In practice, there are two methods currently utilized in commercial beef cattle genetic evaluations to handle genomic information inclusion in BLUP; the single-step genomic BLUP (ssGBLUP) method (Lourenco et al., 2015) and the single-step hybrid marker effects (super hybrid) method (Fernando et al., 2014, 2016; Golden et al., 2016). Regarding the super hybrid marker effects method, threshold capabilities have yet to be developed and as such, genetic evaluations that use this methodology are currently unable to produce genomic evaluations for single-step threshold models. In the case of the RAAA and AGA genetic evaluations for HP, a post-analysis blending method for genomic information is used instead of a single-step method which is not ideal.

An alternative approach to evaluate non-linear or binary records is to use random regression models (RRM) which are more readily adaptable for the inclusion of genomic information and can effectively handle binary data (Kang et al., 2017; Golden et al., 2018). The most common use of RRM in commercial genetic evaluations are implemented in traits where longitudinal data are observed (e.g. daily milk records, calving records), as they are especially proficient in accounting for the covariance structure of repeated records over time (Mrode, 2014). In addition, RRM can better incorporate data from contemporary groups with no variation and thus eliminates the need to discard data with ECP (Golden et

al., 2018). The use of RRM is not strictly limited to longitudinal data and has been shown to be effective at evaluating traits with single observations (Englishby et al., 2016; Speidel et al., 2018; Sanchez-Castro, 2021).

Due to the potential viability of RRM as a method of evaluating HP, this dissertation explored the development of a RRM prototype genetic evaluation in a multi-breed population of beef cattle. Considering the challenges associated with evaluating binary data, the need for single-step genomic inclusion in large-scale genetic evaluations, and the added difficulty of accounting for breed differences and potential heterosis effects, we hypothesized that the application of an RRM for the prediction of HP in a multi-breed population would be the preferred method. As such, the objective of this dissertation was to investigate the development of a multi-breed RRM genetic evaluation for heifer pregnancy in beef cattle.

The specific objectives are outlined below:

1) Investigate and evaluate current data collection practices among IGS partner breed associations and determine appropriate recommendations for standardization of HP data collection. Presently, data are reported to IGS via a secure file transfer portal with fields for exposure (Exposure: 1 = Exposed, 0 = Not Exposed), pregnancy status (Pregnancy: 1 = Pregnant, 0 = Not Pregnant), and a breeding pasture contemporary group identifier. These data are reported to IGS by the breed association or registry service partners and labeled with an international identity using the International Committee of Animal Recording (ICAR) standards for global animal identification.
2) Investigate culling and productivity codes obtained from whole herd reporting (WHR) systems as a potential means of obtaining more appropriate HP phenotypes that are directly indicative of fertility.
3) Compare threshold and linear models on same-breed populations in a pedigree-based genetic evaluation of binary HP observations for pregnancy success.

4) Estimate breed and heterosis effects for HP in a multi-breed population of heifers using threshold and linear models in a pedigree-based genetic evaluation of binary HP observations for pregnancy success.
5) Investigate an alternative definition of HP using RRM approach for the evaluation of HP by calving week compared to threshold or linear models that represent pregnant/non-pregnant phenotypes.
6) Compare validation results using the cross-validation procedures described by Legarra and Reverter (2018), where potential genetic evaluations censor recent phenotypes to compare whole and partial populations to determine which evaluation method is the most appropriate for development.

Across studies, variance components were compared and used to benchmark justification for model selection. Potential models were validated using cross-validation procedures (Legarra and Reverter, 2018) and Pearson correlations for estimated breeding values (EBV). Beef Improvement Federation (BIF) accuracy were compared across evaluation methods.

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CHAPTER 2 - LITERATURE REVIEW

Heifer fertility represents a primary influence on the profitability of a beef cow-calf enterprise. Reproductive rates determine the number of calves born and thus influence the amount of beef product produced at the commercial level, driving income for cow-calf operators. Commercial producers also risk losing investment in the development of yearling heifers that do not breed (Clark et al., 2005). A primary concern is the cost to develop heifers to reach appropriate body weight prior to breeding, and heifers that fail to conceive consume feed resources without providing income (French et al., 2013; Sterry and Halfman, 2020). Heifers that are late-bred produce lighter weight calves and have less opportunity to breed back to calve in the subsequent season (Lesmeister et al., 1973). As such, late-bred and open heifers are typically culled in commercial settings and as a result, genetic progress in a beef herd may be slowed. Replacement heifers are the next generation of genetic progress in a cow herd and heifers with superior genetic merit for performance traits that fail to become pregnant are culled, thus reducing the selection intensity of a breeding program and failing to make optimal genetic progress (Bourdon, 2000). Therefore, within a genetic improvement context and in relationship to the profitability of conventional cow-calf operations selling calves at weaning, improvements in fertility traits (heifer and cow) have been estimated to be up to 4-fold more important than improvements in end-product traits (Melton, 1995b; Formigoni et al., 2002).

2.1 Economic consequences of heifer fertility

The greatest economic value to commercial cow-calf producers is increased weaning rate, because without a calf to sell, no other characteristic has much meaning or economic value (Melton, 1995a). Cattle do not calve until 2 years of age at the earliest, and so the costs to feed and develop heifers can be significant. Beef producers will borrow against the future profits of an animal, by paying for the developmental costs of a heifer – and will only recoup some of that investment when pounds of calf are sold (Wathes et al., 2014). Essential to this financial strategy is that heifers are exposed (via natural

service or AI) to be bred near a year of age and successfully become pregnant to calve at 2 years of age. Heifers that fail to wean a calf represent a lost investment because infertile heifers will result in reduced revenue (Clark et al., 2005; Prevatt et al., 2018). Beef producers will have typically paid for the developmental costs of a heifer before determining fertility status, and heifers that do not become pregnant do not give producers the opportunity to market a calf to offset those developmental costs. For this reason, many beef producers will cull open heifers as they would otherwise need to incur the cost to continue feeding the animal for up to one additional year without any income from the sale of a calf (Ball and Peters, 2004; Walmsley et al., 2018). The ability of a female to reach maximum economic efficiency is predicated on the number of calves born and raised in her life (Grossi et al., 2008; Speidel et al., 2018a). Nunez-Dominguez et al. (1991) demonstrated the improved economic efficiency of beef heifers that calve at 2 years of age versus 3 years of age, highlighting the importance of earlier age at first calving in beef heifers as producers would need to keep females for an additional 2-3 years to reach maximum economic efficiency for females first calving at 3 versus 2 years of age.

Ensuring heifers calve first at 2 years of age places greater emphasis on first service conception via artificial insemination (AI) (Barth, 1993). French et al. (2013), reported that heifers that calve early due to AI or via natural service (NS) stay in the herd longer and wean a greater number of calves compared to heifers that calve later in the herd due to NS only. Furthermore, calves born to early-calving heifers also weigh more at weaning as those calves were older at weaning age. The combination of a higher weaning weights and producing more calves in a lifetime for earlier-calving heifers results in females with greater lifetime revenue (French et al., 2013). For these reasons, traits influencing heifer fertility have been identified as economically relevant traits (ERT) for genetic selection in beef cattle (Golden et al., 2000; Bormann et al., 2006).

Genetic improvement measures of reproductive ability are commonly accepted as necessary to include in most beef cattle breeding objectives due to economic relevance (Barth, 1993; Golden et al., 2000; Olesen et al., 2000; Ball and Peters, 2004). Heritability estimates for many reproductive traits used to describe beef heifer fertility are typically lowly heritable (Cammack et al, 2009). As such, genetic

selection for fertility-related traits in beef heifers have not seen major gains with phenotypic selection due to low heritability (Moorey and Biase, 2020), and perhaps an overemphasis on the evaluation and selection of weight traits (Garrick and Golden, 2009).

2.2 Factors affecting heifer fertility

Reproduction is the outcome of numerous biological interactions and physiological responses resulting from mating a sire and dam (Hopper, 2014). Successful reproduction is dependent on many factors that require the capability of sires and dams to achieve each critical stage of reproductive development (Foote, 2003). As such, heifer fertility is a complex trait made up of numerous biological processes and environmental factors (Corah and Lusby, 1998; Cammack et al., 2009; Wathes et al., 2014; Kelley et al., 2020). Reproduction encompasses a wide range of physiological processes and requires the precise coordination and integration of multiple organs functioning in unison (Figure 2.1; Evans, 2011). Perhaps the simplest strategy to classify sources of variation in cattle fertility are by dividing them into environmental, management, and genetic causes (Venter et al., 1973).

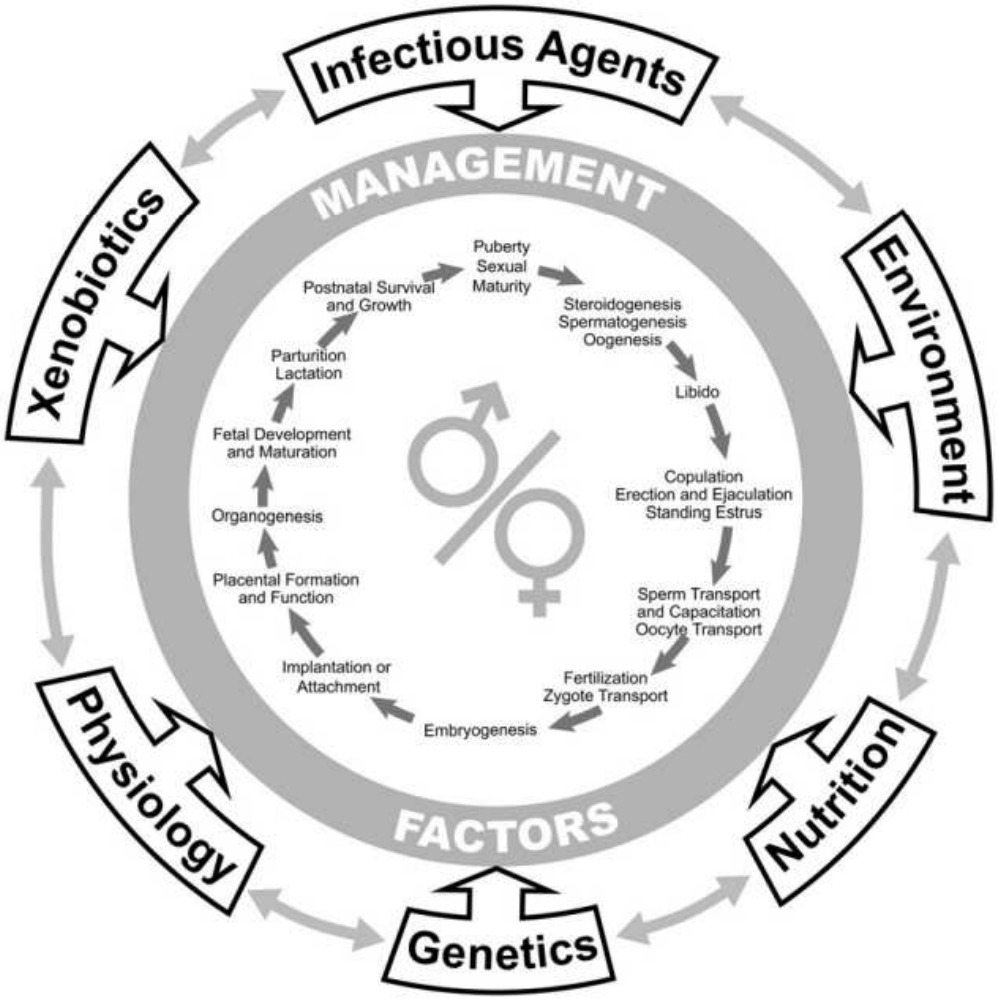

Figure 2.1. Continuum of developmental stages and reproductive processes (Evans, 2011; Adapted from Evans T. J. Reproductive toxicity and endocrine disruption)

2.2.1 Environmental influences

The performance, health, and well-being of cattle are strongly affected by climate (Krishnan et al., 2017), and as a result, environmental conditions are a crucial factor affecting heifer fertility (Thatcher, 1974; Gwazdauskas et al., 1974). Environment represents more than location or a contemporary group, as it is the sum of the temperature, rainfall, pasture availability, and many other factors to which animals are exposed (Copley et al., 2022). The environment can then be defined as the physical place and conditions in which an animal is surviving, as well as the maternal influence of an animal's dam which develops into

physiological effects that we can observe and measure (Duggan, 2023). Environmental factors affecting heifer fertility can include; temperature, humidity, solar radiation, atmospheric pressure, density of nutrients in grazing pastures, precipitation, and day length (Gwazdauskas et al., 1974; Brugemann et al., 2013), however temperature, non-supplemental nutrition and precipitation tend to be the most impactful environmental influences (Thatcher, 1973; Corah and Lusby, 1998; Robinson et al., 2006; Duggan et al, 2022).

2.2.1.1 Temperature

Weather and ambient temperature change with the seasons and is an unavoidable influence in beef cattle management. Exposure to environmental conditions such as heat, and cold stress alters the energy and dry matter intake requirements of developing heifers (NRC, 2001) and can influence the onset of puberty, estrous activity, and pregnancy status. Since tropical and subtropical regions of the world are being more utilized to contribute to food production globally (Thatcher, 1973), much of the research on ambient temperature effects in beef cattle has focused on heat stress. Calving season stress associated with high temperatures and humidity decreases pregnancy rates in cattle (Sprott et al., 2001). Heat stress affects the fertility and reproduction of cattle by compromising the physiological reproductive tract, through hormonal imbalance, decreased oocyte quality, poor semen quality, and decreased embryo development and survival (Krishnan et al., 2017). Ingraham et al. (1974) showed that pregnancy rates in dairy cows declined from 55% to 10% when the temperature-humidity-index increased from 70 to 84. Vincent (1972) reported that heat stress delayed puberty in heifers, caused anestrus in cows, depressed estrous activity, induced abortions, and increased perinatal mortality.

The decrease in reproductive function from heat stress is most likely due to elevated body temperatures (Figure 2.2) which influence hormonal regulation (Krishnan et al., 2017), and cause irregularities in ovarian function, expression of estrus, oocyte health, embryonic development (Biggers et al., 1987; Lucy, 2002), decreased intensity of estrus, failure to ovulate, lack of implantation, embryo disintegration, and fetal abortion (Stott, 1974; West, 2002). In climate-controlled metabolism chambers,

Dunlap and Vincent (1971) reported 0% conception in beef cows that had an average body temperature of 40°C or above, whereas Biggers et al. (1987) reported pregnancy rates of 82, 67, and 55% for cows with body temperatures of 38.9, 39.2, and 39.8°C, respectively. During extremely hot periods in southern U.S. states, there can be an 8-10% drop in first service conception and overall conception rates, but this is more likely caused by embryonic mortality rather than a temperature effect on conception rates (Corah and Lusby, 1998). The proportion of cows in which embryonic death occurs is believed to be much higher in tropical or hot and humid environments compared to those developed in more temperate zones (Stott and Williams, 1962), and as such, strategies to overcome these challenges must be implemented through improved management practices (Hansen and Areechiga, 1999) or genetic selection. To this extent, Moghaddam et al. (2009), reported that cows receiving short-term cooling measures prior to breeding had 16.7%-33.4% higher pregnancy rates in heat-stressed dairy cows. Additionally, tropically adapted *Bos indicus* breeds of cattle experience fewer damaging effects on embryonic survival under heat stress conditions compared to *Bos taurus* breeds of cattle (Silva et al., 2013).

The effects of heat stress are less pressing in more temperate regions (Lucy, 2002), where pregnancy rates are highest in the spring with the absence of cold and heat stress (Mercier and Salisbury, 1974; De Kruif, 1975). Amundson et al. (2006) demonstrated the optimal temperature-humidity index and minimum temperature levels to avoid reductions in pregnancy of beef cows. Cold stress has been documented to negatively influence conception rates (Chebel et al., 2007), and particularly the fertility of beef sires (Gwazdauskas, 1984; Corah and Lusby, 1998). Though admittedly, there is less literature on the effects of cold stress compared to heat stress suggesting, that at least in females, the effects of cold stress are less pressing than heat stress relative to reproduction. Seasonal breeding is not an option for dairy systems; however in U.S. beef systems, seasonal breeding has been a solution to overcome many of the challenges of temperature stress on cow fertility (Deutscher et al., 1991; Lucy, 2002; Donovan et al., 2003).

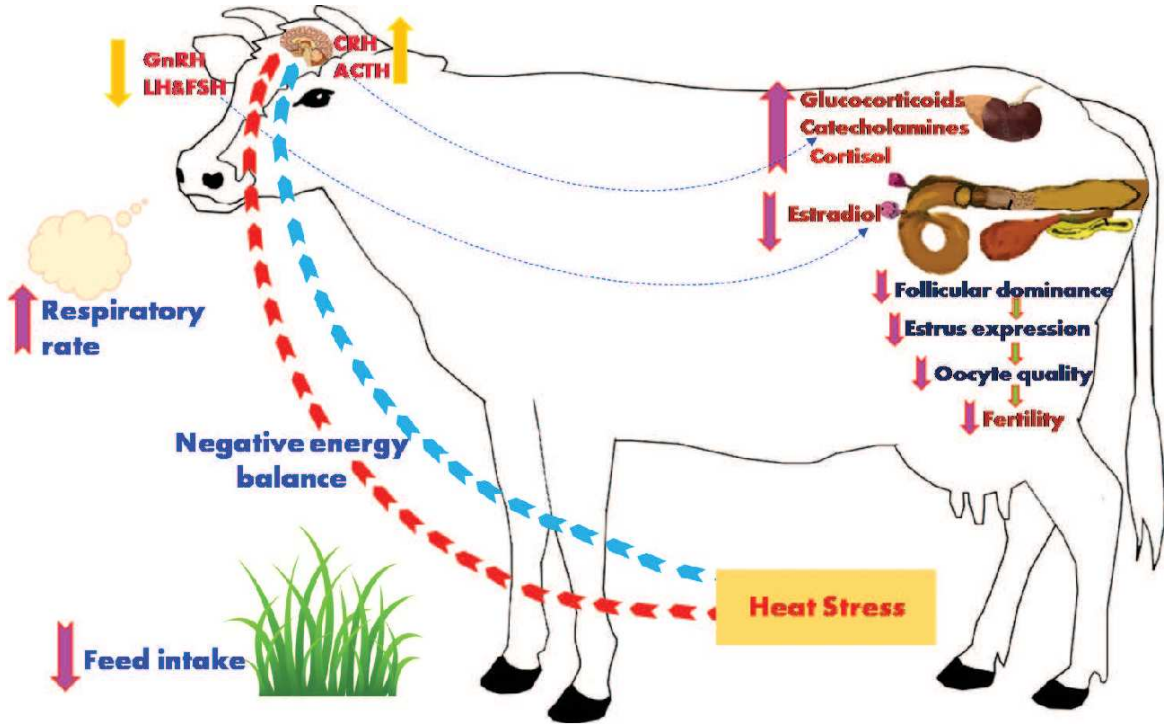

Figure 2.2. Schematic representation on the influence of heat stress on hormone regulation and reproductive performance in cattle (Krishnan et al., 2017).

2.2.1.2 Nutrition

The influence of environment on the sequence of events leading to puberty in heifers is dictated largely by the nutritional status of the animal and related effects on growth rate and development (Patterson et al., 1992). As such, nutritional management of beef cattle can have a profound effect on reproduction (Short and Bellows, 1971; Short et al., 1972; Short and Adams, 1988) as it supplies the specific nutrients required for oocyte development, ovulation, fertilization, embryo survival and the establishment of pregnancy (Robinson et al., 2006). From a herd perspective, pregnancy rates in heifers depend on the number of heifers displaying estrus early in the breeding season, and nutrition is one of the major limiting factors controlling hormone regulation to reach puberty and maintain estrus (Frisch, 1984; Short and Adams, 1988). Byerley et al. (1987) reported that heifers should experience 2 or 3 estrous cycles before onset of the breeding season because fertility of the first estrus is less than in subsequent estrous cycles. As such, heifers need to reach a body weight that meets maintenance energy requirements

and allows for pubertal development, because most reproductive failures can be attributed to inadequate or thin body condition. This is because the processes of reproductive tract development, maintaining estrus, conception, fetal development and calf delivery are physiological processes that require the availability and utilization of large quantities of energy (Selk et al., 1988).

Successful reproduction relies on the effects of adequate nutrition on sexual maturation and are related to the timing and release of luteinizing hormone (LH), as it is necessary for the growth of ovarian follicles to the preovulatory stage (Schillo, 1992). The release of prepubertal LH stems from the anterior pituitary in a pulsatile manner (Rahe et al., 1980) controlled by the luteinizing hormone releasing hormone (LHRH) being released into the hypothalamic-hypophysical portal vascular system by neurosecretory cells located in the hypothalamus (McCann, 1974). This pulsatile release of LH is the result of a decrease in the responsiveness of the hypothalamic-pituitary axis to estrogen negative feedback (Kinder et al., 1987) which stimulates the development of ovarian follicles to the preovulatory stage (Schillo, 1992). Dietary energy restriction has been shown to suppress the release of LH in cattle (Imakawa et al., 1987) as it disrupts the functional intake of nutrients necessary for the hypothalamic-pituitary-gonadal axis to regulate the production and release of hormones. This complex endocrinological relationship is dependent on a host of diverse macro- and micronutrients: such as phosphorus, vitamin A, β-carotene, protein and energy (Dunn and Moss, 1992). A well-balanced diet and nutrition plan in developing heifers can ensure the proper intake and utilization of crucial macro- and micronutrients necessary for successful reproduction, whereas inadequate nutrition can impair reproductive function and delay the onset of puberty in beef cattle (Foster and Olster, 1985; Day et al., 1986)

Numerous studies have reported inverse correlations between postweaning growth rate and age at puberty (Arije and Wiltbank, 1971; Short and Bellows, 1971; Wiltbank et al., 1985). Therefore, it is commonly recommended that heifers be developed to reach a weight between 60 and 65% of the expected mature body weight (MBW) before breeding (Martin et al, 2008). Selk et al. (1988) suggested that body condition score (BCS) precalving and at the start of the breeding season, along with body weight changes between 2 and 4 months before parturition, had profound effects in subsequent pregnancy rates of range

beef cows. Body condition scores (BCS) represent a numerical system of classifying the relative fatness and body composition of beef cattle and can range from 1 to 9, with 1 being extremely thin and 9 being extremely fat (Herd and Sprott, 1986). The BCS can be an excellent estimator of body fat percentage in beef cows (Selk et al., 1988). Because estimating percentage of MBW can be difficult in replacement heifers, BCS serves as a more accessible classification, and it is recommended that heifers be managed to a BCS of 6 prior to calving. Dickinson et al (2019), reported that heifers managed to a BCS of 6 had a higher percentage of being pregnant via AI and natural service compared to heifers managed to a BCS of 5. Energy restrictions during late pregnancy results in thin BCS at calving and extends the interval to first postpartum estrus in beef cows (Richards et al., 1986).

Nutritional supplementation is a practice that can overcome environmental challenges and provide necessary trace minerals necessary for reproductive development. Heifers need to be developed to reach 60%-65% of their mature body weight, and appropriate supplementation of trace minerals is essential for maintaining growth, immune function and reproductive performance in beef cattle (Lamb et al., 2007). Dunn and Moss (1992) described the functional roles of macro- and micronutrients for reproductive maturation in heifers which highlights the importance of nutritional supplementation in nutrient-deficient environments. Low winter supplementation is shown to adversely affect age at first calving and lifetime productivity (Pinney et al., 1972). Additionally, heifers fed an NRC supplemental energy diet for gain during the first 21 days after AI breeding were shown to have higher first service conception compared to heifers on an NRC maintenance diet (Arias et al., 2012). Therefore, appropriate nutritional supplementation strategies may provide beef cattle managers greater opportunity to maximize reproductive potential in heifers (Graham, 1991; Bailey et al., 2001; Lamb et al., 2007).

Another nutritional concern that can result in pregnancy loss is the presence of toxins in the diet. Toxic materials in the diet can affect reproductive success by causing abortions, interfering with libido, estrus, oogenesis, or spermatogenesis causing emaciation and subsequent abnormal behavior, birth defects, and increasing the time between parturition and rebreeding (James et al., 1992). There are many potential toxicants adversely affecting livestock health and reproductive success (Diekman and Green,

1992; James et al., 1992: Panter et al., 2002; Evans, 2011), but perhaps the most prevalent and concerning are mycotoxins, and nitrates associated with some plant species (Evans, 2011). Mycotoxins are a mold that reduces the quality of grain but more importantly synthesizes a chemical substance that impairs growth and reproductive efficiency in livestock (Diekman and Green, 1992). Mycotoxins are most concerning during wet conditions or when feed has become exposed to excess moisture which is ideal for fungal growth and typically leads to depressed fertility in mild cases and abortions in extreme cases (Thomas and VanWye, 2021). Nitrates in the soil can be assimilated into plants in adverse weather conditions (cold stress and drought) and can be naturally found in other common livestock forages at varying degrees of severity (Evans, 2011). Overconsumption of nitrate-dense forages results in nitrate accumulation in the blood which decreases oxygenated blood, and can result in depressed animal performance and abortions, and in severe cases, death (Thomas and VanWye, 2021).

2.2.1.3 Climate conditions

Beef cattle are one of the most well-suited animals for food production in harsh environments and are found in environmentally diverse regions of the world for this reason. Factors such as drought, poor-forage quality, high temperatures or humidity, high elevation, and parasite load are all common problems affe cting biodiverse cattle producing regions (Drouillard, 2018). Drought commonly found in harsh environments creates a lack of readily available food sources and is typically accompanied with heat stress, consistently suppress female fertility. Copley et al. (2022) reported that a temperature humidity index (THI) of 65-70 had a significant, negative effect on first lactation pregnancy rate, heifer pregnancy and puberty at 600 days of age; and that average daily weight gain had a significant, positive relationship with heifer and first lactation pregnancy. When rainfall is limited or highly variable from year to year, the ability to capture nutrients from forage in arid or semiarid and convert them into pounds in developing heifers is reduced (Vavra et al., 2000). The western U.S. has several unique features that shape the beef cattle industry in those states, with the principal feature consisting of arid and high elevation rangeland with variable climates from year to year (DelCurto et al., 2000). Animals that are less genetically adapted

to the stresses of surviving in high elevation have a negative relationship with heifer pregnancy, and when compounded with less than average annual rainfall can exacerbate this negative relationship (Duggan et al, 2021). Conversely, tropical and subtropical climates come with the added risk of parasitic influences. Internal and external parasites such as biting flies and ticks can transmit diseases and lead to reduced reproductive performance in moderate cases, and in more extreme cases with high parasitic loads can result in losses of confirmed pregnancies (Thomas and VanWye, 2021). Producers can respond to these climatic influences that hinder reproductive performance through management strategies and genetic selection.

2.2.2 Management practices

Lowly heritable traits are influenced more by the environment and management of livestock populations compared to more moderately or highly heritable traits. Fertility traits are considered lowly heritable (Cammack et al., 2009), which underscores the importance of proper management practices to ensure successful reproduction. Reproductive management is the sum of the decisions and actions made by a producer to create an environment that optimizes the opportunity for a female to become pregnant. Many management procedures have been developed to maximize the reproductive potential of beef heifers such as: nutritional management and supplementation, identification of reproductive maturity by physiological and morphological indicators, defining an appropriate breeding season, and the implementation of estrus synchronization programs (Moorey and Biase, 2020). To increase the efficiency of cow-calf production systems, reproductive management strategies and the implementation of new technologies may help overcome limitations in beef heifer fertility.

Producers usually aim to breed replacement heifers by 15 months of age in *bos taurus* breeds of cattle in order to calve at 24 months of age (Wathes et al., 2014). However, to optimize the number of opportunities for a heifer to become pregnant, an appropriate breeding season length must be established (Frasier and Pfeiffer, 1994). A longer breeding season ensures numerous opportunities for conception but lengthens the subsequent calving window. Late-bred females in an extended calving season have a higher

risk of being culled due to fewer pounds of weaned calf and an anestrus period overlapping with the next breeding season in turn reducing opportunities for subsequent re-breeding. Shorter breeding seasons ensure a shorter calving season but will also likely result in fewer pregnant females compared to a longer duration breeding season. Limited breeding and calving seasons generally result in increased calf production and greater production system efficiency (Duetscher et al., 1991). Restricting breeding seasons to better align with the time of year that optimizes calf survival, calf growth, feed availability, and seasonal beef commodity pricing opportunities should also be considered (Frasier and Pfeiffer, 1994).

2.2.2.1 Reproductive technologies

Artificial insemination, estrous synchronization and fixed-time AI (TAI), semen and embryo cryopreservation, multiple ovulation and embryo transfer (MOET), in vitro fertilization, sex determination of sperm or embryos, and nuclear transfer are all examples of reproductive technologies that have been developed to greatly improve the reproductive efficiency of beef productive systems across the globe (Dahlen et al., 2014). Despite the development and adoption of these reproductive technologies in other beef-producing countries, many U.S. beef producers have failed to adopt these strategies and it's suggested more than 90% of the U.S. beef cattle operations use natural mating as their primary reproductive strategy (Lamb and Mercadante, 2016). In the United States, slow adoption rates of these technologies may result in a future loss of international market share of beef products as other nations take advantage not only of the additional pounds of beef that can be produced but also the improved quality of beef that can be realized through incorporation of reproductive technologies and resultant genetic improvement (Dahlen et al., 2014).

Artificial insemination techniques have evolved from fresh semen being deposited directly into the vagina (as would be the case with natural service), to more intensive procedures which require sperm preparation and cryopreservation. The ability to preserve sperm viability until insemination was a major advance in the establishment of organized AI efforts (Moore and Hasler, 2017). The basic premise of sperm cryopreservation is to slow down and inhibit metabolic activity by cooling to extremely low

temperatures, preserving the structure of sperm cells with an egg-yolk phosphate buffer to survive extended freezing, and the addition of antibiotics in extenders to prevent bacterial-growth. With these methods, viable semen can be preserved indefinitely (Polge and Rowson, 1952). However, not all ejaculate has been shown to be viable for both natural service mating and freezing so standards for evaluating bull fertility and semen survivability have been established (Williams, 1920; Salisbury et al., 1943; Elliott, 1978; Kastelic and Thundathil, 2008). Breeding soundness exams (BSE) establish that natural service bulls must have: a scrotal circumference greater than 30 cm at 15 mo of age (when most bulls are turned out into breeding pastures;), more than 30% of progressively motile sperm and less than 30% morphologically abnormal sperm (Chenoweth et al., 1993). For commercially cryopreserved semen, ejaculates typically require at least 65% motile and morphologically normal sperm (DeJarnette et al., 2022), which places greater emphasis on sperm motility compared to natural service mating.

Artificial insemination in replacement heifers is a practice that can concentrate the breeding and calving season, and help improve pregnancy rates (Patterson et al., 1992). Estrus detection and the interval to first service conception are some of the most important considerations for heifer reproductive efficiency, thus estrus detection and TAI synchronization protocols have been developed (Lucy et al., 1986: Larson et al., 2006). The beef industry relies heavily on estrous synchronization for AI programs to ensure heifers have reached an appropriate age and are at the correct stage of the estrous cycle. Additionally, few beef producers are willing to monitor expression of heat in groups of heifers for extended periods of time, so additional care must be taken to ensure optimal conception as there are numerous factors affecting the response to hormonal regimens of TAI (Lamb, 2005). Implementation of synchronization protocols by beef producers has been met with resistance compared to dairy operators, due to labor concerns and complicated protocols (Lamb and Mercadante, 2016) Thus limiting the frequency of animal handling and eliminating the need for estrus detection are the two primary factors when considering implementation of TAI strategies in beef herds.

Early estrus synchronization protocols focused on regressing the corpus luteum (CL) with an injection of prostaglandin $F_{2\alpha}$ (PGF) to induce luteolysis followed by estrus detection (Lauderdale et al.,

1974). However, this still required additional labor to monitor the expression of estrus, and and included the potential for failure to induce luteolysis in prepubertal heifers or females in anestrus, diestrus, and metestrus phases. Estrus detection is a time-consuming and repetitive task that is problematic to employ in beef production systems (Stevenson et al., 1996). As a response to females in various phases of the estrous cycle, administration of gonadotropin-releasing hormone (GnRH) was shown to increase the concentration of luteinizing hormone (LH) and ovulation of the dominant follicle (Carter et al., 1980; Pursley et al., 1995). Thus, a combination of GnRH followed by an injection of PGF 7 days later was used to synchronize the follicular wave and induce luteolysis which stimulated a more concentrated level of estrous activity in groups of females (Lamb and Mercadante, 2016). This additional control of the follicular waves was the foundation for modern estrus synchronization protocols that eliminated the need for estrus detection and maximized the reproductive efficiency of heifers in various stages of the estrous cycle.

Modern estrous synchronization protocols have evolved to include a second injection of GnRH 48 hours after the PGF injection to induce ovulation of the dominant follicle, and the inclusion of exogenous progesterone (P4) released through a controlled internal drug release (CIDR) device to prevent ovulation before the PGF injection (Lamb et al., 2001; Larson et al., 2006; Lamb and Mercadante, 2016). There are numerous TAI protocols featuring different timing intervals to accommodate the varying physiological processes involved in the estrous cycle, but perhaps the most common protocol used in dairy and beef cattle is the “Ovsynch” (Pursley et al., 1995). As summarized by Lamb and Mercadante(2016), the Ovsynch protocol consists of three hormonal injections: the first, GnRH, is intended to reset and synchronize follicular waves, the second, PGF, given 7 days later, induces luteolysis, and the third, GnRH, given 36 to 48 hours after the PGF injection, induces ovulation of the dominant follicle. Artificial insemination is performed 16 to 24 hours after the second GnRH administration (Figure 2.3).

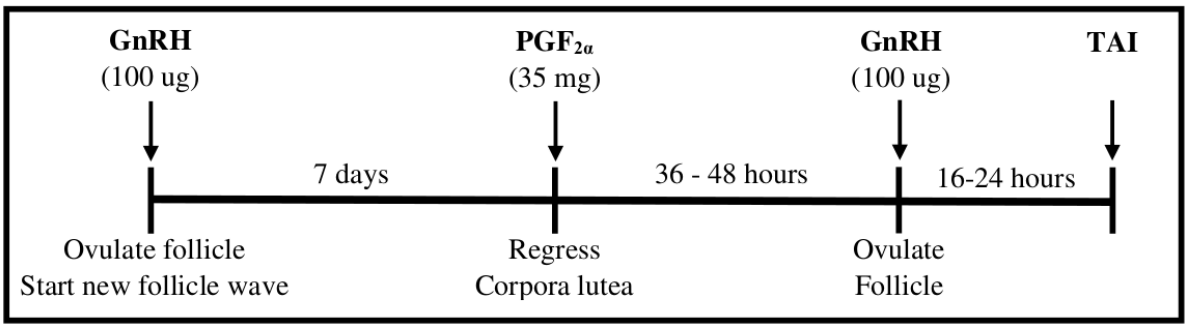

Figure 2.3. Description of the timing and physiological action of each hormonal injection applied in the Ovsynch protocol (Adapted from Pursley et al., 1995).

The Ovsynch protocol was successful in revolutionizing TAI and improving reproductive efficiency, but the ovulation response in anestrus females was poor and varied by the day of the estrous cycle (Vasconcelos et al., 1999; Atkins et al., 2008; Lamb and Mercadante, 2016). A modification of the Ovsynch protocol led to the inclusion of P4 released through a CIDR device in a new estrus synchronization protocol called "7-day Co-Synch + CIDR," resulting in improved or equivalent fertility rates (Lamb et al., 2001; Geary et al., 2001; Larson et al., 2006). The inclusion of an intravaginal P4 CIDR during the 7-day interval between initial GnRH and PGF injections were shown to increase pregnancy rates by 9 to 10% (Lamb et al., 2010). The Ovsynch and Co-Synch protocols both eliminate the need for estrus detection, improve fertility opportunities for heifers in a fixed breeding season and concentrate calves being born earlier in a calving season (Larson et al., 2006). Extensive research is ongoing to better understand the physiological processes involved in the estrous cycle, and in an effort to combine expertise and encourage research cooperation across research institutions, the Beef Reproduction Task Force (BRTF) was formed in 2002. The BRTF releases an updated chart of recommended estrous synchronization and TAI protocols for beef cows and heifers annually (Figure 2.4).

The physiological and morphological identification of sexual maturity in heifers can lead to increased reproductive efficiency as not all animals may have reached an appropriate developmental status before the breeding season begins. Reproductive tract scoring (RTS) systems can help categorize heifers according to uterine and ovarian development (Anderson et al., 1991) and can better predict

reproductive outcomes in seasonally bred beef heifers (Holm et al., 2016). An RTS includes the measurement of the length and diameter of the left and right ovaries, presence and diameter of a CL, largest follicle diameter, uterine horn diameters and the transverse and vertical diameters of the pelvis. These measurements are then translated into a categorical scoring system ranging from 1 (pre-pubertal, infantile tract) to 5 (pubertal, CL present). Several reports have demonstrated a strong and positive relationship between RTS and pregnancy rates (Holm et al., 2009; Gutierrez et al., 2014; Dickinson et al., 2019).

Many advancements in reproductive biotechnologies have led to greater opportunities for genetic advancement, a better understanding and monitoring of the estrus cycle, and greater manipulation of reproductive outcomes through sexed semen and cloning methods (Moore and Hasler, 2017), however many of these may not directly contribute to improved pregnancy rates in beef heifers. Recent developments in estrus monitoring and detection devices have revolutionized the dairy industry (Johnson et al., 2011; Piñeiro et al., 2018; Schweinzer et al., 2019), but have translated poorly for use in the beef industry due to the stark differences between beef and dairy production systems. Embryo transfer (ET) and superovulation technologies have allowed for rapid multiplication of animals and propagating elite female genetics but pregnancy rates using ET methods are often substantially lower compared to AI and natural service mating (Aherin et al., 2018).

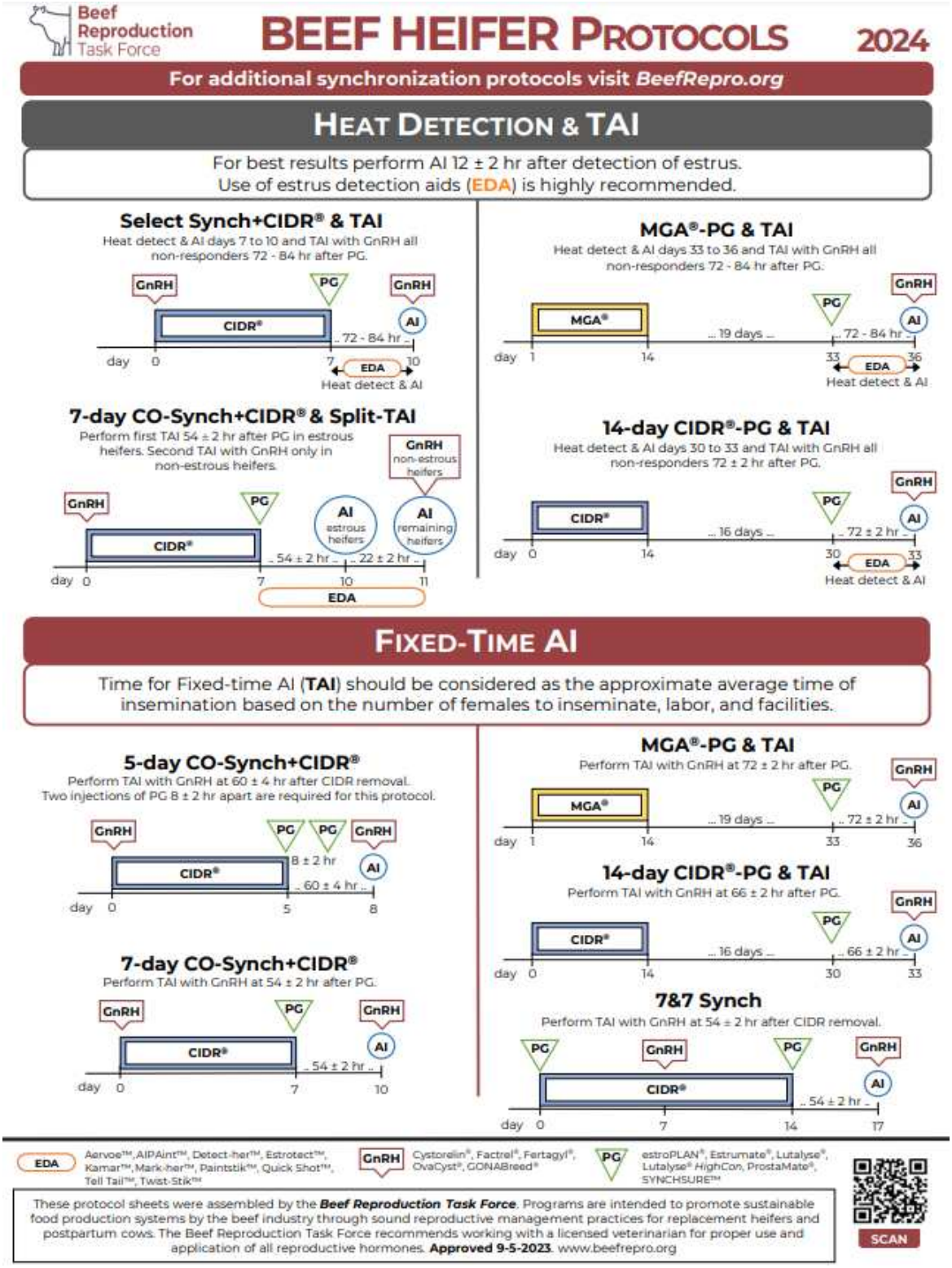

Figure 2.4. Beef Reproduction Task Force (BRTF) chart of recommended estrous synchronization and timed artificial insemination protocols for beef heifers (Beef Reproduction Task Force 2024, University of Nebraska-Lincoln, Lincoln, NB).

2.2.2.2 Herd health

Managing herd health is an important component of optimizing reproductive efficiency and overall performance. Reproductive diseases are estimated to cost approximately $441 to $502 million annually for U.S. beef producers, which is six times more costly compared to respiratory diseases (Bellow et al, 2002). There are many vectors that can introduce reproductive disease into a herd (Givens, 2006). However, the most common reproductive diseases in cattle are brucellosis, leptospirosis, vibriosis, trichomoniasis, infectious bovine rhinotracheitis (IBR) and bovine viral diarrhea (BVD). These infectious diseases are most commonly contracted as new animals are purchased from external production systems and are introduced to a herd, though parasites can also carry these diseases (Sprott and Field, 1998). Perhaps the best way to minimize pregnancy loss and infertility as a result of disease is through preventative herd health management practices (Thomas and VanWye, 2021) such as adequate animal surveillance, biosecurity thresholds and standards, and effective vaccination programs (Givens, 2006). In the case of highly pathogenic, zoonotic diseases like Brucellosis, control and eradication programs continue to be integral to managing the spread of disease (Zhang et al., 2018).

2.2.2.3 Determining pregnancy

Determining pregnancy prior to parturition is an important management tool because it allows breeders to identify earlier which females are candidates for culling due to reproductive failure, and more appropriately allocate feed resources towards pregnant females. The traditional method of pregnancy determination is by transrectal palpation, which includes a technician inserting their arm into the rectum and feeling the reproductive tract for pregnancy indicators (Carpenter et al., 2023). Pregnancy indicators include the presence or absence of fluid in the uterus, the tone (firmness) of the uterine horns, enlargement of a single or both uterine horn(s), and the presence of an embryo/fetus and accompanying vesicle attached to the uterine horn (Bekele et al., 2016). The relative size of the fetus helps indicate the number of days into gestation. Typically, pregnancy determination is practiced from 40 to 60 days after first artificial insemination in intensive cow herds (Lucy and Poock, 2012), and more commonly 120-150

days in commercial beef herds to coincide with weaning (Dyer, 2017). An earlier pregnancy diagnosis provides greater opportunity for proactive management decisions. However, the historic concern with transrectal palpation at younger embryonic ages is a higher risk of early embryonic/fetal death due to the trauma induced by the procedure, however Romano et al., (2007) reported no statistical evidence to support this argument. Rather, the more pressing concern with rectal palpation has been the lack of skilled technicians, typically veterinarians, to perform the procedure and a general lack of specificity in determining the true age of the fetus.

Since the 1990's the use of ultrasound (US) as a diagnostic tool for pregnancy determination has been utilized to capture additional sensitivity and in part relieve the lack of skilled technicians (Lucy and Poock, 2012). Transrectal ultrasonography is a procedure that uses sound waves to create a picture of the reproductive tract by inserting a small, lubricated probe into the rectum (Pierson et al., 1988). Compared to rectal palpation, the biggest difference for US is the need for specialized and expensive equipment. The skills required of an ultrasonographer demand basic eye-to-hand coordination, experience locating reproductive structures, and detailed working knowledge of reproductive anatomy and pathology (Pierson et al., 1988). With an appropriate placement of the US probe, results are gathered via actual visualization of the fetus but US application also introduces the possibility of reproductive tract scoring and diagnosis of potential reproductive issues. With the development of more affordable, and smaller machines, US for pregnancy determination has become an appealing alternative and can be implemented by less skilled cattle practitioners while providing greater accuracy than rectal palpation (Quintela et al., 2012).

2.2.3 Genetic influence of fertility

Genetic selection is used to improve economically relevant traits in beef cattle populations so long as there is evidence of genetic variability. The mechanism used to describe a population's level of genetic variability is termed heritability, which is the proportion of additive genetic variance relative to the phenotypic variance in a population. In selection, relatively fast genetic progress can be achieved in traits with moderate to high heritability such as growth, and carcass quality (Torres-Vázquez et al., 2018).

As has been established, fertility in beef cattle is a complex process with many influences from an animal's environment and management and as such, the heritability of traits directly related to female reproduction are typically low and genetic selection is much slower relative to growth and carcass traits. Despite low heritability, there is enough genetic variability in cattle populations to make meaningful genetic improvement for fertility traits (Mackinnon et al., 1990; Doyle et al., 2000; Cammack et al., 2009). The challenge, however, with selecting for improved heifer fertility rests in the difficult nature of collecting the phenotype and appropriately modelling the trait in a genetic evaluation. Pregnancy phenotypes can only be observed in females and at much older ages compared to routine growth and carcass phenotyping efforts. Heifer pregnancy (HP) is traditionally defined as the binary observation of a heifer conceiving and remaining pregnant to palpation, given exposure during the breeding season (Doyle et al., 2000). Using this definition of HP, the characterization of the additive genetic control of heifer pregnancy has been well established, with heritability estimates ranging from 0.12 to 0.30 using maximum *a posteriori* probit threshold models (Doyle et al., 2000; Cammack et al., 2009; Boldt et al., 2018).

Despite the depth of investigation into HP, implementation of HP genetic evaluations in national beef cattle evaluations (NCE) have been met with numerous challenges. The first obstacle has been a lack of robust whole herd reporting (WHR) data systems among breed registries, presenting complications with accurate phenotyping and establishing appropriate contemporary groups (Cammack et al., 2009). Heifers initially enrolled/registered as calves at a breed association will typically be paired with their heifer mates in contemporary group, but if any of those heifers are sold as bred yearlings the ability to assign a pregnant phenotype becomes a challenge, and as a result the record is often thrown out or doesn't exist. The second challenge surrounding HP genetic evaluations is due to the binary nature of pregnancy status phenotypes being appropriately applied to best linear unbiased prediction (BLUP) methodology (Gianola, 1982; Gianola and Foulley, 1983). Pregnancy status phenotypes are binary categorical response variables and thus not normally distributed and may lack homogenous variance across contemporary groups, datasets or populations (Gianola, 1982). As a result, numerous related fertility traits have been

suggested as alternatives for NCE (Cammack et al., 2009), and different statistical methods to more appropriately model the traits (Jamrozik et al., 2013; Sánchez-Castro et al., 2020).

2.2.3.1 Age at puberty

Among relevant and measurable fertility traits, age at puberty has been suggested as a substitute trait for genetic improvement of heifer fertility due to its low correlation with other productive traits and low genotype by environment interactions (Martin et al., 1992). Reproductively efficient heifers reach puberty earlier and can potentially conceive earlier in a breeding season (Cammack et al., 2009), however in some *bos taurus* breeds of cattle it could be argued that virtually all heifers will have reached puberty before first exposure (Dow et al, 1982). Differences in mean age at puberty between breeds are documented, as well as between crossbred and purebred heifer populations indicating that heterosis and breed play an important role in the genetics of age at puberty (Laster et al., 1972; Gregory et al., 1979; Gregory et al., 1991). Breed differences are most notable between *bos indicus* and *bos taurus* breeds of cattle, where typically *bos indicus* heifers may be bred a full year later than their *bos taurus* counterparts (Lopez et al., 2006).

Puberty is defined as when ovulation is accompanied by visual signs of estrus and subsequent normal luteal function (Perry, 2016). Other traits closely related to age at puberty used as predictors of heifer fertility include age at first corpus luteum (Engle et al., 2019), age at first estrus, and age at first breeding (Herring and Patterson, 1997). However, age at puberty and related traits are difficult to observe in commercial settings and as such, limits the amount of data being collected by producers for use in a genetic evaluation (Cammack et al., 2009). There are also conflicting results on the additive genetic relationship between age at puberty and heifer pregnancy (Gregory et al., 1991; Moser et al., 1996; Evans 1999). Martin et al. (1992) proposed that when entire contemporary groups of heifers reach puberty prior to the onset of a breeding season, heifers that reached puberty at younger ages have no advantage in conception over their contemporaries that reached puberty at older ages.

2.2.3.2 Age at first calving

Age at first calving (AFC) is routinely recorded through accurate birth date record keeping and is highly genetically correlated with age at subsequent calving and calving interval (Gutiérrez et al., 2002). Females that calve earlier in a calving window produce heavier calves at weaning and are cycling at a higher rate for the subsequent breeding compared to later-calving contemporaries (Funston et al., 2012). Thus, AFC is a critical element to heifer rebreeding success and can influence the overall lifetime profitability of an animal in a herd (French et., 2013). Various studies have investigated the genetic component of age at first calving (Gutierrez et al., 2002; Bormann et al., 2010; Berry et al., 2014; Brzakova et al., 2020; Pardo et al., 2020; Gonzalez–Murray et al., 2021); and typical of most fertility traits, age at first calving (AFC) is reported as a lowly heritable trait (0.08-0.37). Age at first calving is a simple trait to observe as it only requires birth dates to determine the phenotype which is simply the difference in days between a heifer's birth date and her progeny birth date. This means that AFC encompasses pubertal age, conception rate at various services, and gestation length on an individual. Age at first calving is a cheaper and more accessible phenotype to measure but may lack the precision of traditional HP evaluations. Virtually no beef production systems expose heifers at the onset of puberty and instead rely on fixed breeding seasons to provide opportunity for pregnancy. Thus, the expression of AFC is predicated upon the initial date of first exposure and the length of the breeding season. Heifers that are born later in a calving season and therefore younger in their cohort at first exposure would have more opportunity to have a younger AFC, and heifers that are born earlier in a calving season would be older than their contemporaries at first exposure and therefore have less opportunity for younger AFC (Bormann et al., 2010). The differences in breeding season variability and differing lengths of calving windows would prove challenging to properly account for in a genetic model. This, in addition to heifers that fail to conceive at 2 will have no observation for AFC and not be included in any evaluation for the trait, suggesting AFC is limited in its capabilities as a prediction of actual fertility. For these reasons there are no examples of commercially available genetic evaluations of AFC in North American *Bos taurus* breeds of cattle.

2.2.3.3 First-service conception

Artificial insemination is an important tool for beef operators to leverage genetically superior genetics and provides an opportunity for heifers to have an earlier opportunity to become pregnant with estrous synchronization and TAI protocols when used in tandem with natural service exposure. First-service conception rate (FSCR) is then a reproductive measure that provides producers an opportunity to identify those females that become pregnant at first breeding compared to heifers that require multiple opportunities to become bred (Cammack et al., 2009). Heifers that can conceive on their first opportunity at breeding are going to calve earlier, which will give them a greater chance to breed back the following year (Lesmeister et al., 1973). The definition of FSCR is then defined as the probability of a heifer to conceive in response to her first AI and maintain the pregnancy after the end of the breeding season (Sánchez-Castro et al., 2020). Similar to HP, data collection for FSCR phenotypes involves allocating binary categorical responses to heifers that were successful in becoming pregnant with only one AI (e.g. 1=successful, 0=unsuccessful; Borman et al., 2006). Heritability estimates for FSCR range between 0.03 to 0.22 (Dearborn et al., 1973; Bormann et al., 2006; Sánchez-Castro et al., 2020). Variability in breed composition, age at time of breeding, scale of the trait, and statistical methods for modelling the trait are likely reasons for the differences in heritability estimates for FSCR. Regardless, with moderately low heritability, there is an opportunity to genetically select for improved FSCR in beef heifers which could initiate an increase in the use of AI in the beef industry.

The adoption of AI technology in cattle is approximately 80% of all dairy cows in North America, compared to only 4% in beef cattle (Colazo and Mapletoft, 2014). Perhaps the main reason for low adoption of AI technology in beef cow herds is that the protocol for estrous synchronization requires numerous visits through a chute, costly pharmaceuticals, and is time and labor intensive. Mediocre conception rates from TAI coupled with the cost of synchronization have led to slow adoption among beef producers (Parkinson, 2004; Lamb et al., 2010), and in recent years a significant decline of beef semen sales has been observed (NAAB, 2022). With fewer beef herds utilizing AI technology, it can

become a challenge to develop NCE for FSCR because of a lack of reliable data streams, and the trait still faces many of the same modelling challenges as HP.

2.2.3.4 Stayability

Increasing longevity of beef cows by decreasing the proportion culled due to reproductive failure provides an efficient process to maintain a cow herd and can reduce the number of replacements needed to sustain a constant herd size (Roberts et al., 2015). Perhaps the most successful development of a genetic evaluation for the improvement of female fertility and longevity in beef cattle is Stayability (STAY). Originally defined as the ability of a cow to remain in the herd until a specific age given the opportunity to reach that age (Hudson and Van Vleck, 1981), STAY today is generally evaluated as the probability that a cow will remain in the herd until 6 years of age given she calved as a 2-year-old (Brigham et al., 2007). The age of 6 is an important benchmark as it represents the financial breakeven point where a female has successfully recouped her developmental and maintenance costs (Snelling et al., 1995; Brigham et al., 2006). The ability of cows to stay in the herd until 6 years of age or longer greatly reduces the demand for replacement heifers in a production system, which reduces the need to pay for developmental costs, decreases the incidence of dystocia in calving heifer populations, and increases the average weaning weight of marketed calves (Garrick, 2006; Jamrozik et al., 2013)). This represents a significant economic benefit and in herds with a low proportion of females remaining in the herd until 6 years of age, a 1-unit change in herd STAY EPD can have significant financial consequences (Enns et al., 2005).

The main problem with the current definition of STAY is that a female must reach a benchmark of 6 years of age to obtain a phenotype, representing a significant time lag in data collection and accurate genetic evaluation (Jamrozik et al., 2013). Stayability EPD were typically derived using a single trait threshold model which ignored variation in disappearance rate prior to, or after the age of 6, and as a result the sire of a female would be at least 8 years old before a phenotype was observed. This time lag and the gaps in female disappearance was reflected in poor accuracy of prediction and provided little

utility for the selection tool among seedstock breeders wanting to maximize genetic progress by using younger sires (Jamrozik et al., 2013). Garrick (2006) proposed a multiple trait approach by accounting for stayability at each age as separate correlated traits as a solution to the time lag problem and increasing prediction accuracy earlier in life. This approach necessitates the need for robust WHR programs to more appropriately account for the fate of every animal and the reason for leaving the herd since not all disposals may be fertility related. A continuation of this approach by modelling each STAY age as longitudinal data in a random regression model (RRM) was later proposed by Jamrozik et al. (2013), which has become the statistical method of choice for modern STAY genetic evaluations (Golden et al., 2018; Oliviera et al., 2020; Culbertson and Atkins, 2021). Presently, the American Angus Association (AAA), American Hereford Association (AHA), and the International Genetic Solutions (IGS) genetic evaluation which services over 20 beef breed associations globally produce a genetic evaluation for STAY or a related definition of STAY using RRM.

Depending on the end age point, breed type, and statistical method used, heritability estimates for STAY range from 0.03 to 0.36 (Snelling et al., 1995; Martinez et al., 2005; Beckman et al., 2006; Cammack et al., 2009; Jamrozik et al., 2013; Oliviera et al., 2020). Snelling et al. (1995) reported heritability estimates for STAY at ages 2, 5, 8, and 11 (given the female calved at least once) of 0.02, 0.14, 0.09, and 0.07 respectively using a threshold animal model and Angus cattle data from the Colorado State University John E. Rouse Beef Improvement Center. Martinez et al. (2005) reported heritability estimates for STAY to consecutive ages (given she had a calf as a 2-year-old) from 1 to 6 years ranging from 0.05 to 0.19 using a linear animal model and ranging from 0.09 to 0.30 using a threshold animal model in Hereford cattle. Beckman et al. (2006) reported heritability estimates for STAY in a two-trait linear animal model with BCS at ages 2, 3, and 4 of 0.19, 0.15, and 0.08 respectively in Red Angus females. Jamrozik et al. (2013) tested alternative statistical methods for the evaluation of STAY and reported heritability on the underlying liability scale that a female would reach age 8 with an estimate of 0.24, and heritability estimates ranging from 0.36 for STAY age 2 to 0.12 at STAY age 8 using a linear RRM in Canadian Simmental females. Jamrozik et al. (2013) reported the linear RRM was the model that

gave the best fit to the binary data and overcame some of the challenges of significant data collection time lag observed in traditional threshold model methodology. Stayability represents a measure of the productivity and sustained fertility of a cow from first calving to culling, and regardless of the definition and statistical method for genetic evaluation STAY relies first that a female has had the opportunity to become productive in the herd by having her first calf at 2 years of age. This is the reason why independent HP and STAY evaluations exist.

2.2.3.5 Scrotal circumference

As described, genetic selection for improved cow fertility can be challenging due to considerable time lag in data observation, imprecise phenotypes, as well as only being able to observe phenotypes on females that are pregnant or have produced a calf. A general solution to overcoming observing sex-limited traits is to select on a genetically correlated indicator trait observed in the opposite sex, and there have been reports that scrotal circumference in males is favorably genetically correlated with age at puberty (Brinks et al., 1978; Smith et al., 1989). Scrotal circumference is used to predict the quality and quantity of spermatozoa-producing tissue and is related to age at puberty (Cammack et al., 2009). A scrotal circumference measurement of 28-30 cm is the general benchmark to indicate the onset of puberty in males and is reported as a highly heritable trait (Evans et al., 1999). Brinks et al. (1978) reported a –0.71 genetic correlation between scrotal circumference and age at puberty in females. Morris et al. (1992) reported genetic correlations between scrotal circumference and heifer puberty traits had an average of -0.39 ± 0.22 for age at first estrus, -0.19 ± 0.20 for standardized age at first estrus, and -0.39 ±0.20 for weight at first estrus.

The general assumption is that reducing the age at puberty in heifers leads to higher pregnancy rates due to a greater chance the female is cycling before a breeding season. Therefore, phenotypic selection for increased scrotal circumference could be a means to improving female fertility through indirect selection if heifers are not cycling at the onset of a breeding season. However, more recent results in literature provide conflicting results on the additive relationship between scrotal circumference and HP

(Gregory et al., 1991; Martin et al., 1992; Moser et al., 1996; Evans et al., 1999). In general, the largest discrepancies between the genetic relationship of HP with scrotal circumference exist between *Bos indicus* and *Bos taurus* breeds of cattle. Eler et al. (2004) reported genetic correlations between HP and scrotal circumference in Nelore cattle at 0.20 when using two different contemporary group definitions. McAllister et al. (2011) reported a near-zero genetic correlation estimate between HP and scrotal circumference of 0.05 (±0.09) in Red Angus cattle. The increase in the genetic correlations reported in *Bos indicus* breeds of cattle are likely a result of increased genetic variability of reaching puberty at 14 months of age compared to Bos taurus breeds where puberty is already largely established by that age (Eler et al., 2004). Since reaching puberty at younger ages doesn't generally translate to improved conception (Martin et al., 1992; Evans et al., 1999; Martínez-Velázquez et al., 2003), it is presumed the genetic relationship between scrotal circumference and age at puberty does not translate to improvements in heifer pregnancy.

2.2.3.6 Novel fertility traits

Opportunities to better characterize heifer fertility exist by evaluating novel and genetically correlated indicator traits, and by doing so, may accelerate the rate of genetic gain of heifer pregnancy by increasing the accuracy and volume of phenotypic data contributing to genetic evaluations (Meier et al., 2021). If an additive genetic relationship between a novel fertility trait and reproductive performance exists, then there is potential to include that novel trait in future genetic evaluations especially if a novel trait can be observed earlier in life. For these reasons, interest in the evaluation of novel fertility traits in dairy cattle such as the resumption of cycling postpartum, estrus behaviors, physiological and conformational indicators, and pregnancy loss is increasing (Petersson et al., 2007; Bamber et al., 2009; Berry et al., 2014; Fleming et al., 2015; Gobikrushanth et al., 2017; Lucy, 2019). Table 2.1 provides a list of heritability estimates for novel traits. In general, all traits were low to moderately heritable. As many of these traits are newly studied, genetic correlations with traditional pregnancy are largely unknown. However, in some cases favorable phenotypic observations were observed between a novel fertility trait

and pregnancy outcomes. For example, Young et al. (2017) and Madureira et al. (2020) reported increased pregnancy outcomes per AI in beef and dairy heifers with more favorable reproductive tract scores initially developed by Anderson et al. (1991). Lucy (2019) reported on a variety of novel traits favorable impact on pregnancy outcomes in dairy cattle.

A strong candidate novel measure that increases the rate of genetic gain and improves prediction accuracy for fertility evaluations should have higher heritability than existing fertility traits, be more easily characterized or observed earlier in life, and have a moderate to high additive genetic relationship with reproductive performance and pregnancy rates. The ability to measure more novel fertility traits has been accelerated largely due to technological advancements in reproductive monitoring applications including ear sensors, ankle pedometers, movement collars, and video cameras. However, with these devices and software programs comes an additional cost to beef producers, and in some herds the marginal improvement in pregnancy rates may not justify the cost.

Table 2.1. Summary of heritability estimates (h^2) for novel fertility traits related to heifer pregnancy.

Trait	h^2	*r* with HP*	References
Age at puberty	0.14	-0.33	Snelling et al., 2012
Anogenital distance	0.37		Gobikrushanth et al., 2019
Anovulation	0.16-0.19		Bamber et al., 2009
Antral follicle count	0.31-0.44	-0.55	Snelling et al., 2012; Walsh et al., 2014 Fleming et al., 2015
Embryonic loss	0.02		Carthy et al., 2015
High activity/movement	0.01-0.09		Ismael et al., 2015
Luteal activity	0.14-0.30		Veerkamp et al., 2000; Royal et al., 2002; Petersson et al., 2007; Berry et al., 2014; Tenghe et al., 2015
Number of services	0.01-0.07	-0.56	Berry et al., 2014
Reproductive tract scoring	0.31		Anderson et al., 1991
Reproductive health traits			
Multiple ovulation	0.03		Berry et al., 2014
Ovarian cysts	0.02-0.12		
Puerperal disease	0.2-0.14		
Silent heat	0.01-0.06		
Uterine Score	0.10		Carthy et al., 2015

* If reported by authors in same manuscript.

2.2.3.7 Relationship with other performance traits

Considering that many breeding objectives place most of the emphasis on growth and carcass characteristics, it is important to understand the implications of genetic selection for other performance traits on reproductive performance. Intensive selection for milk yield from the 1950's to the early 2000's led to a substantial decline in pregnancy rates in the U.S. Holstein herd (Peñagaricano, 2020), and unfavorable negative genetic correlations between production traits (e.g. milk yield, milk fat, growth, and health) and functional traits such as fertility are well documented (Berry et al., 2003; Kadarmideen, 2004; Windig et al., 2006). Berry et al. (2003) reported a genetic correlation between cumulative milk yield to

day 240 and pregnancy status at day 63 of –0.22 (±0.14), which suggests that selection in the direction of increasing milk yield may reduce pregnancy rates. Selection programs placed an overemphasis on milk production and neglected fertility which resulted in an industry-wide decrease in reproductive performance. With the introduction of selection tools such as Daughter Pregnancy Rate (DPR) and improved management practices, reproductive performance saw meaningful improvement over the last 20 years (Figure 2.5).

Within the beef industry there are many traits that directly impact profitability on beef cattle enterprises. Optimal selection decisions based on multiple traits must then consider all genetic antagonisms among all ERT of interest to a breeding objective (McAllister et al., 2011). There has been some concern, however, that there is an overemphasis for selection on growth and terminal performance traits in beef cattle (Archer et al., 1998; Garrick and Golden, 2009), with inadequate regard for reproductive fitness and animal health and well-being. There has been little evidence to suggest this overemphasis has led to reduced pregnancy rates like those observed in dairy cattle (Archer et al., 1998; Moorey and Biase, 2020). However, a key difference in production systems between beef and dairy is that beef heifers are typically given many more opportunities to become pregnant with virtually all beef heifers being naturally exposed to sires in at least a 60-to-90-day breeding season. Management strategies such as extended breeding seasons and the beneficial effects of heterosis (Cundiff et al., 1974) can conceal degrading genetic merit for a lowly heritable trait like HP over time, and so it is important to understand the consequences of selecting for growth and terminal traits in beef cattle relative to potential genetic change in fertility.

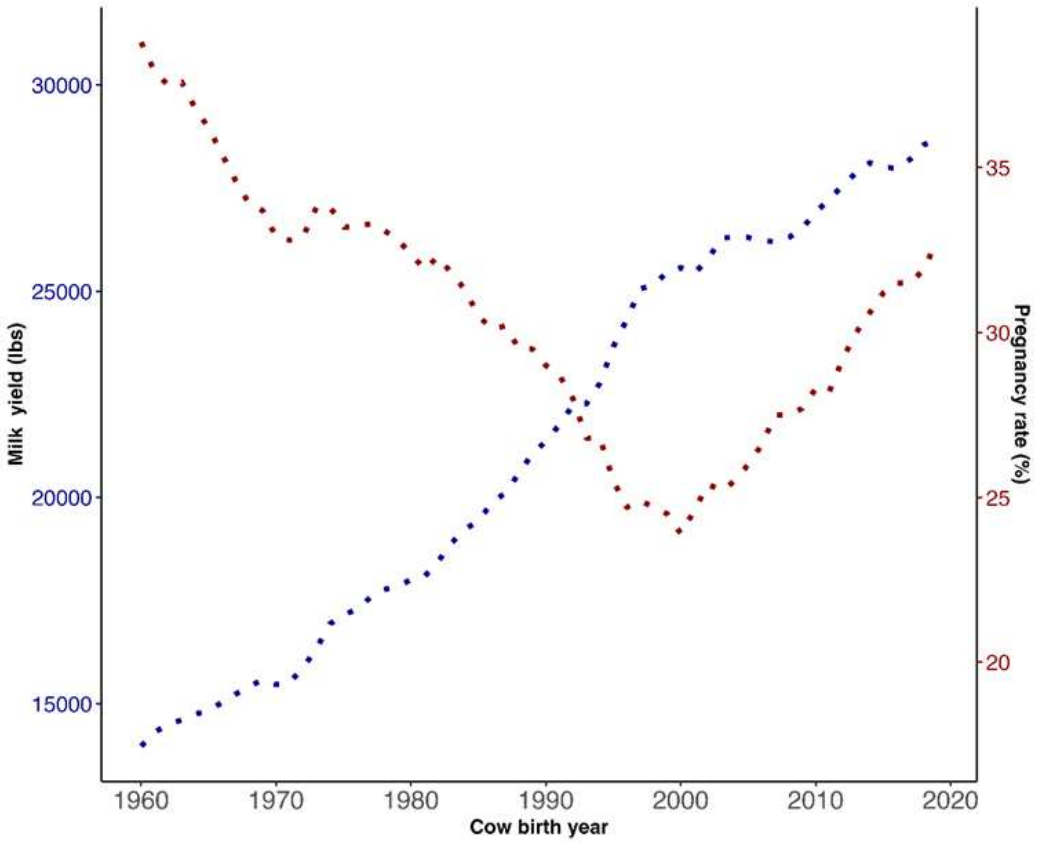

Figure 2.5. Changes in milk yield and pregnancy rate in U.S. Holstein dairy cattle (Source: Council on Dairy Cattle Breeding website (June 2024); https://www.uscdcb.com).

The genetic relationships between growth and other ERT have been established by estimating variance components and genetic correlations between groups of traits; however, there is a growing body of evidence investigating these genetic relationships with reproductive performance. Archer et al. (1998) reported means for pregnancy rates in cattle lines selected for low, unselected (control) and high growth genetics over 10 years of 0.77, 0.85, and 0.86. These results suggest that selection for high growth rate did not compromise reproductive performance; however, the study did not investigate a genetic correlation between growth and HP and females were given a 12-week breeding season providing ample opportunities to become pregnant. Eler et al. (2014) examined the genetic relationship of HP with post-weaning gain (PWG) in Nellore females and reported a genetic correlation of 0.31 (±0.21) between both traits. The positive but weak genetic correlation between HP and PWG provides some evidence that

selection for improved growth performance did not compromise female reproduction in this population of Nellore. Variance components and genetic correlation estimates between HP and performance traits in Red Angus cattle were investigated by Boldt et al. (2018), where weak and positive genetic correlations between HP and weaning weight direct (WWd), and yearling weight direct (YWd) were 0.18 (±0.08) and 0.21 (±0.07), respectively. This provided further evidence that selection for growth performance should not compromise heifer pregnancy.

Genetic correlations between HP and terminal carcass merit were also examined. Short et al. (1990) described the prioritization of energy occurring in a set order in beef cattle starting with; basal metabolism, activity, growth, energy reserves, establishing/maintaining pregnancy, lactation, additional energy reserves, estrous cycle, initiation of pregnancy, and providing excess reserves. The excess energy reserves are accumulated as intramuscular and subcutaneous fat, meaning that measures of fat thickness can serve as indicators of a heifer's ability to be cycling and maintain a pregnancy. Therefore, the genetic relationship of HP with terminal carcass traits such as ultrasound intramuscular fat percentage (UIMF), marbling score (MARB), backfat thickness (BF), and ultrasound backfat thickness (UBF) are important as potential selection for improved MARB and BF may have repercussions on reproductive performance. McAllister et al. (2011) reported a genetic relationship between HP with IMF of 0.13 (±0.09) suggesting that concomitant selection for increased fertility and carcass merit would not be antagonistic. Boldt et al. (2018) reported genetic correlations between HP with ribeye area (REA), BF, MARB, and hot carcass weight (HCW) of 0.21 (±0.21), -0.08 (±0.23), -0.08 (±0.19), and -0.03 (±0.25), respectively. High standard errors are common between estimates involving actual carcass data, and so Boldt et al. (2018) also investigated the genetic relationship between HP with ultrasound ribeye area (UREA), UBF, and ultrasound intramuscular fat (UIMF) and reported estimates of 0.16 (±0.08), 0.14(±0.08), and 0.06 (±0.08), respectively. The weak genetic relationship between HP and terminal carcass traits suggests selection for improved carcass performance will not compromise reproductive performance in beef heifers.

2.3 Genetic evaluations for fertility traits

Even though the beef industry has not seen a major reduction in pregnancy rates, there is some concern that improvements in management techniques could conceal eroding genetics for fertility (Amer, 2012; Friggens et al., 2017). Genetic improvement is a long-term endeavor and so genetic selection for improved heifer pregnancy is still a high priority and should be included in most breeding objectives (Enns and Crews, 2008), justifying the need for development of robust HP genetic evaluations. Genetic evaluations for HP have suffered though from limited data reporting, a lack of robust WHR programs, and difficulties with the statistical method for evaluating binary data in a genetic evaluation. Though it is apparent that heifer reproductive fitness is a critical trait for beef operators, a multitude of traits that have been proposed as possible indicators of heifer fertility such as scrotal circumference or age at first calving, but these target traits have not proven useful. Despite a clear and economic justification for the development of NCE for fertility traits, few examples of a successful commercial genetic evaluation for HP exist except for those produced by the Red Angus Association of America, the American Gelbvieh Association, and the American Angus Association.

Collecting phenotypic records for unbiased HP genetic evaluations requires the production records of every replacement heifer in a contemporary group. Whole herd reporting is the collection and reporting of production information on every cow along with the performance data of every calf raised through weaning in a production system. The purpose of WHR programs is to accumulate reproductive and performance data on all animals in a herd and serve as the foundation for many of the fertility trait evaluations in NCE (BIF Guidelines, 2021). The purpose of WHR is not to control which animals are to be registered, but rather have all the information present in a contemporary group to make fair and unbiased comparisons representative of genetic differences. Reproductive data on replacement heifers are typically reported in the form of a heifer exposure inventory which include: breeding season start and end dates, individual exposure status, management group, breeding pasture, disposal information, pregnancy status, and a yearling weight contemporary group definition. Additional useful HP information could also include artificial insemination (AI) service dates, AI sire identification, AI protocol, observed natural

service, and pregnancy results (BIF Guidelines, 2021). Designating breeding season length is for use in genetic prediction models, which generally do not use data from an open-ended breeding season (e.g., >90 days). Some breed associations have developed a HP prediction under the assumption that a heifer with a yearling weight observation is assumed to have been exposed and those that report a calf at 2 years of age were successfully bred to overcome the lack of HP inventory observations (Speidel and Enns, 2015).

Despite the utility of these observations for NCE, phenotypic pregnancy observations have been difficult to collect among the major beef cattle breed associations (Speidel et al., 2018a). Industry adoption of WHR programs in breed association registry services was historically slow among U.S. breed associations since first proposed in the late 1990s. As the need for reproductive fitness genetic evaluations grew, many breed associations began to offer robust WHR programs, and several organizations even now require mandatory WHR from members to take advantage of the unbiased growth predictions and ability to predict EPD for traits like STAY (Krymowski, 2019).

However, common challenges among the existing HP genetic evaluations still include issues with prediction accuracy and time lag before observations are available, as well as the need to more efficiently include molecular information. Because of these reasons there is ample opportunity to improve existing HP genetic evaluations. Additionally, as seedstock populations have diversified to include multiple breeds and composite/crossbred animals the added complexity of multi-breed genetic evaluations should be considered for NCE of fertility traits (Pollak and Quaas, 2005).

2.3.1 Threshold models

The vast majority of existing HP genetic evaluations leverage phenotypes that are binary, categorical response variables for pregnancy status. As such, the most appropriate statistical model for the evaluation of binary observations has been a threshold model (TM). Categorical responses (e.g., 1 = pregnant, 0 = nonpregnant) violate assumptions of normality and do not possess homogenous variance (Gianola, 1982). The threshold model introduced by Wright (1934) can be used to model discrete

variables because it assumes there is an underlying continuous unobservable and a normally distributed trait, called a liability, which becomes discrete (observed scale) when an animal exceeds a particular threshold level for the underlying trait (Falconer and Mackay, 1996). Fernando et al. (1983) described that some of the properties of BLUP do not hold with categorical traits; including the invariance of BLUP to certain types of selection, and the ability of BLUP to maximize the probability of correct pairwise rankings. Gianola and Foulley (1983) developed a Bayesian nonlinear method for sire evaluation of categorical variables based on the threshold concept introduced by Wright (1935), where the probability of a response in a given category is assumed to follow a normal integral with an argument dependent on fixed thresholds and on a location parameter in a conceptual underlying distribution (Figure 2.6).

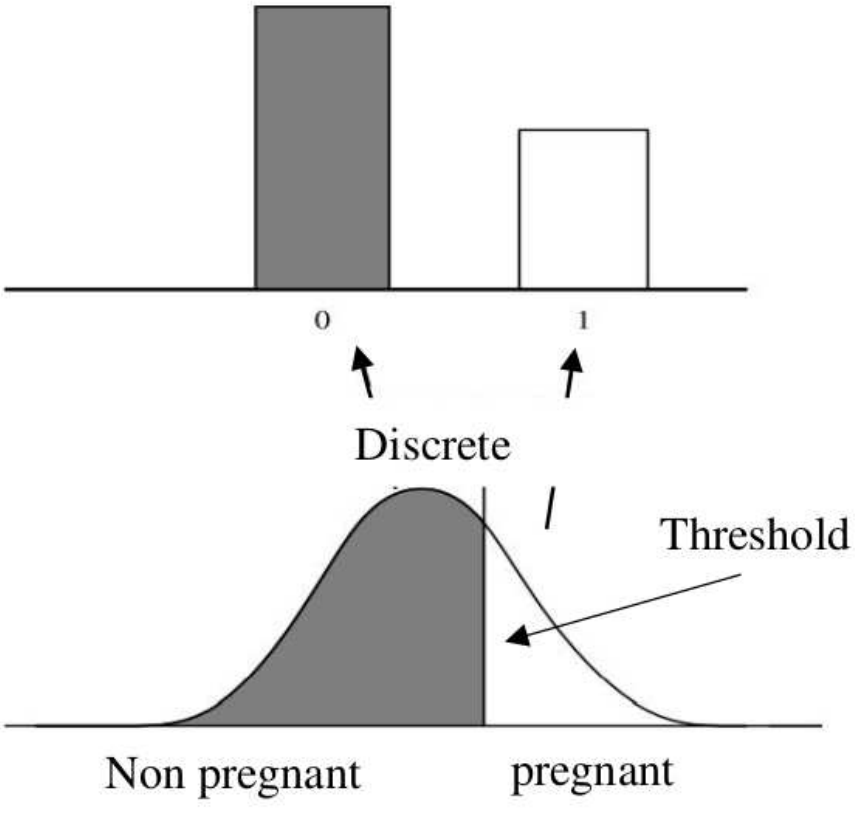

Figure 2.6. Schematic representation of the threshold model, showing the continuous distribution of the underlying liability and the resulting discrete distribution of the observed phenotype (Retrieved from Sánchez-Castro, 2021; Adapted from Felsenstein, 2005).

The general form of a TM for the analysis of a liability as described by Mrode (2014) can be shown in matrix form as:

$$y = Xb + Zu + e$$

Where ***y*** is the vector of a liability (transformed observations) on a normal scale, ***b*** and ***u*** are vectors of fixed and random (sire or animal) effects, respectively, and ***X*** and ***Z*** are incidence matrices relating observations in ***y*** to fixed effects and random animal effects, respectively, and ***e*** represents a vector of unknown residual errors. Since ***y*** is not observed, it is not possible to solve for ***u*** using traditional mixed model equations (MME). In the analysis of a binary trait, with the assumption of a threshold model, differences between levels of fixed effects will correspond to changes in the liability. Therefore, a function to link changes in the liability to changes in the binary trait needs to be incorporated in the MME. Cameron (1997) demonstrated the analysis of a binary trait with a TM using a logit function. Gianola and Foulley (1983) demonstrated the analysis of a binary trait using a system of non-linear equations to find the estimator $\hat{\mathbf{H}}$ that maximizes the log of the posterior density L(**H**), i.e. the mode of the log-posterior density. Given that **H'** = $[t',\ b',\ u']$, where t is the vector for threshold effects. For this model, the variances are assumed to be:

$$var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_\alpha^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

where ***A*** represents the Wright's numerator relationship matrix, ***I*** is an identity matrix, and σ_α^2 and σ_e^2 are the additive and residual variances, respectively. The additive direct genetic variance is trait specific and units are expressed on the underlying scale. Gianola and Foulley (1983) demonstrated that the residual variance is constrained to be equal to 1 to meet the specifications of the maximum *a posteriori* probit TM. The following non-linear iterative system of equations are based on the first and second derivatives, assuming a normal distribution to obtain solutions for *Δt, Δb, Δu.*

$$\begin{bmatrix} Q & L'X & L'Z \\ X'L & X'WX & X'WZ \\ Z'L & Z'WZ & Z'WZ + A^{-1}G^{-1} \end{bmatrix} \begin{bmatrix} \Delta t \\ \Delta b \\ \Delta u \end{bmatrix} = \begin{bmatrix} p \\ X'v \\ Z'v - A^{-1}G^{-1}u \end{bmatrix}$$

where **T, L, W, p,** and **v** involve normal distribution functions, $\mathbf{G} = I\sigma_e^2$ and **W** is a diagonal matrix. This requires differentiating L(**H**) and setting the vector of first derivatives equal to zero and solving for $\hat{\mathbf{H}}$ (Gianola and Foulley, 1983). However, **H** is not linear, so the Newton-Raphson method of iteration is applied so that each set of linear equations are solved successively until solutions converge (when Δ are sufficiently small from one iteration to the next). This system of equations resembles the linear MME, however matrices and vectors due to threshold effects are created differently, and the right-hand sides are a function of **G** and **u** and the equations are solved for differences between consecutive iterations (Mistzal, 1989).

Historically, HP is assessed as a binary threshold trait, with observations being transformed to an underlying normal distribution via a probit link function (Gianola and Foulley, 1983; Harville and Mee, 1984). Van Vleck (1971) suggested an underlying normal distribution of genetic and environmental values has a linear relationship between the genetic value on a normal scale and the genetic value on the binary scale and can be described in an equation as:

$$h_b^2 = \frac{h^2 z^2}{[p(1-p)]}$$

where, h^2 is the heritability on the normal scale, z is the height of the ordinate of the normal distribution at the threshold point which determines whether a binary variable is a one or zero, and p is the frequency of ones. There is extensive research regarding evaluating heifer fertility on the underlying scale. Buddenberg et al. (1989) investigated variance components of heifer pregnancy on both the underlying and observed scales in Angus, Hereford, and Polled Hereford females bred to calve first at 3 years of age. For the Angus, heritability estimates were 0.17, and 0.34 on the observed and underlying scales respectively. For Hereford, heritability estimates were 0.04 and 0.08 on the observed and underlying scales respectively. For Polled Hereford, heritability estimates were 0.05, and 0.10 on the observed and underlying scales respectively. These results suggest that estimating heritability estimates on the underlying scale yielded higher heritability compared to the observed scale. Snelling et al. (1996) reported higher heritability estimates for heifer pregnancy in linecross and Line 1 Herefords using TM

methodology, with an average h^2 of 0.21 and 0.30, respectively. Evans et al. (1999) indicated HP could be included in a bivariate TM with SC, and reported a heritability estimate of 0.14 for HP on the underlying scale in a population of New Mexico Hereford cattle. Doyle et al. (2000) demonstrated TM methodology for the evaluation of HP, and the analysis yielded an average heritability estimate of 0.21 in a population of Angus heifers in Wyoming. In a more recent population of Red Angus heifers with data being provided by the Red Angus Association of America (RAAA), McAllister et al. (2011) reported a heritability estimate of 0.17 on the underlying scale. Boldt et al. (2018) continued the investigation into fertility traits of RAAA animals, and with a decade more records, reported an average heritability estimate of 0.12 for HP using TM methodology in bivariate animal model mixed model. Heritability estimates from these studies are generally low, further attesting to HP being a lowly heritable trait in cattle populations.

Genetic evaluations based on TM analysis have produced a larger rate of response to selection than those based on linear models (Meijering and Gianola, 1985; Mistzal et al., 1989). However, the potential advantage of TM has been impaired by computing difficulties, and a slow or lack of convergence when all responses for a given class of a fixed factor occur in an extreme category (Misztal et al., 1989). Obtaining solutions from the Bayesian equations requires an intensive iterative process (Meijering and Gianola, 1985) and the computational costs are higher for TM compared to traditional linear, continuous trait evaluations. Misztal et al. (1989) estimated the cost of TM to be 3 to 5 times higher than linear model evaluations due to the intensive iterative process where a linear set of equations must be solved during each iteration. As computing power has improved in recent years, the more pressing concern for TM are situations where there is an extreme case problem (ECP), exhibited when observations for a fixed effect all fall into the same category (e.g. all observations of 0 or 1). This presents poor convergence criteria as such classes tend to gravitate towards $\pm \infty$ or 0 as iteration proceeds (Misztal et al., 1989).

Potential solutions to overcome ECP were presented by Harville and Mee (1984), including treating fixed effects as random variables or ignoring/eliminating those observations experiencing ECP. Treating fixed effects as random variables is considered restrictive and may violate the assumptions

required, whereas the second option of removing records in extreme categories would lead to distorted inferences because the edited data would not be representative of entire populations (Misztal et al., 1989). Consequently, genetic predictions that do not use all the available information often yield lower accuracies in comparison to statistical methods capable of incorporating all available observations (Sánchez-Castro et al., 2019). Furthermore, TM are not readily adaptable to the incorporation of genomic information in modern single-step genetic evaluations (Speidel et al., 2018b) unless genomic relationship matrices are used as seen in the single-step genomic BLUP (ssGBLUP) method (Legarra et al., 2009). In populations with a large number of genotyped animals, ssGBLUP becomes challenging because the inverse of the genomic relationship matrix (GRM) is required. Adding extra genotyped individuals to a GRM incurs linear computing costs and quadratic memory constraints (Misztal, 2016). A solution presented by Misztal (2016), involves decomposing the population arbitrarily into core and non-core individuals, with the number of core individuals equal to that dimensionality, so that breeding values of noncore individuals can be derived from recursions on breeding values of core individuals from the GRM. An equivalent method to ssGBLUP involves estimating single nucleotide polymorphisms (SNP) marker effects that are then included in a strategy where marker covariates for non-genotyped animals are estimated and combined with marker effects of genotyped individuals (Fernando et al., 2014), commonly referred to as the super hybrid marker effects model. Under normality, this method yields results identical to ssGBLUP but does not require computing the GRM or its inverse. However, TM have not yet been adapted into the framework of super hybrid marker effects models (Fernando et al., 2016).

2.3.2 Random regression models

Random regression models have become common for the analysis of longitudinal data or repeated records on individuals over time and are the preferred statistical method for the evaluation of cow fertility traits (Jamrozik et al., 2013; Sánchez-Castro et al., 2017; Oliviera et al., 2020). Random regression models (RRM) were introduced by Henderson (1982) and Laird and Ware (1982) as an alternative to overcome problems of over-parametrization in multi-trait analysis and better evaluate traits

with longitudinal data. The most successful example of a RRM has been the genetic evaluation of test-day milk production records in dairy cattle (Ptak and Schaeffer, 1993), but more creative applications for RRM across many biological situations in animal breeding are being investigated (Schaeffer, 2004). RRM allows the ability to evaluate changes in genetic variability over time because the statistical methods recognize the covariance structure between serial observations of the same trait on the same animal. Schaeffer and Dekkers (1994) showed this by extending the regression coefficients of the fixed regression model to also include random animal effects for the prediction of milk test-day records. This made it possible to illustrate the average shape of the lactation curve for a specific herd, year, and season, and to show how each animal's lactation curve deviated from the average shape. The RRM capability to accurately account for the changing correlation structure has been demonstrated to improve prediction accuracy by 5.9% compared to evaluations using multivariate models (Meyer, 2004). The only major disadvantage of RRM evaluations is the volume of data to be analyzed is much larger. The general form of a RRM as described by Mrode (2014) is shown in matrix form as:

$$y = Xb + Qu + Zpe + e$$

where ***y*** is a vector of repeated observations measured on individual animals, ***X*** is an incidence matrix relating observations in ***y*** to fixed effects and fixed regression coefficients, ***b*** is a vector of solutions for fixed effects and fixed regressions, ***Q*** is an incidence matrix of covariates relating observations in ***y*** to random additive genetic regression coefficients, ***u*** is a vector of random regressions for additive direct genetic effects, ***Z*** is an incidence matrix of covariates relating observations in ***y*** to permanent environmental regression coefficients, ***pe*** is a vector of random permanent environmental regression coefficients for each animal, and ***e*** is a vector of random residuals which includes temporary environmental effects for each observation. The variances assumed for RRM are then:

$$var\begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & I \otimes P & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where ***A*** is Wright's numerator relationship matrix, ***G*** is the (co)variance matrix of the additive genetic random regression coefficients, ***I*** is an identity matrix with an order equal to the total number of

observations, ***P*** is the (co)variance matrix of the permanent environmental random regression coefficients, and σ_e^2 is the variance of random residuals. The **G** and **P** matrices are of the order of polynomial fitted for the animal and permanent environment effects. In some cases, the random residual variance $I\sigma_e^2$ structure can vary with elements that depend on different observational endpoints. This modified residual variance structure was presented by Jamrozik et al. (1997) as:

$$var[e] = diag\{\sigma_{ek}^2\}$$

where k is equal to the total number of differing residual variances. In the example presented by Jamrozik et al. (1997), k equaled a number from 1 to 29, such that when days in milk (DIM) are between 5 and 20, then k=1; when DIM are between 21 and 30 then k=2; and k increases by 1 for every 10 days thereafter except for k=29 when DIM are between 291 and 305 days. Thus, the residual variance structure has 29 different values on the diagonal depending on the number of days in milk. If the assumption of homogenous variance does not hold across all stages of production, a modification such as this one presented should then be made to the model which allows the residual variance to change between those stages of production. Ignoring the necessity of modelling a heterogenous residual variance structure could result in over- or under-estimations of heritability values (Olori et al., 1999). The assumption of homogeneous residual variance has no effect on permanent environmental variance (López-Romero et al., 2003). When a homogeneous random residual variance is assumed, then R = $I\sigma_e^2$ (Schaeffer, 2004; Speidel et al., 2010; Oliveira et al. 2019). Assumptions about the distributions of ***y*** and other random variables are not necessary to derive BLUP or the MME when ***y*** is normally distributed and the (co)variances are known (Goldberger, 1962; Henderson, 1984), however, in situations where the variance components required to solve the MME are not known in advance, it is necessary to estimate those from the dataset (Schaeffer, 2004). Variance components of a RRM can be estimated using traditional restricted maximum likelihood (REML) processes (Hofer, 2011) or Bayesian (Jamrozik and Schaeffer, 1997) methods. Once the variance components are obtained, Mrode (2014) illustrated that the MME for a RRM are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Q & X'R^{-1}Z \\ Q'R^{-1}X & Q'R^{-1}Q + A^{-1} \otimes G & Q'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Q & Z'R^{-1}Z + P \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \\ \widehat{pe} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Q'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

These RRM are an extension of multiple-trait repeatability models but with a key difference that the random genetic animal effects can vary over time periods without increasing model complexity. The covariates in Q and Z are specialized to better account for changes in the covariance structure between successive observations of longitudinal data and have a phenotypic correlation with the observations in ***y***. Longitudinal traits are recorded multiple times during an animal's lifetime and therefore, expressions of the phenotypes of these traits are linked to specific time points (Oliveira et al., 2019). The initial structure of these covariance functions was laid out by (Kirkpatrick and Heckman, 1989; Kirkpatrick et al., 1990; Kirkpatrick et al., 1990) and defined them as the infinite-dimensional counterpart to covariance matrices used in standard multivariate analyses. Speidel et al. (2010) listed the advantages of these covariance matrices over conventional methods as:

1. Covariance functions can describe a trait at all time points, even if measurements were not taken on specific days, rather than at a finite number of data points.
2. Covariance functions help to reduce errors in calculating the response to selection. Conventional methods only select on a specific age window (for example birth weight or weaning weight); however, when selection on a part of the curve is performed, the entire trajectory is changed through the genetic correlation (selecting on increased birth weight has the correlated effect of increasing weaning weight). Covariance functions help account for the correlated responses observed at other data points.
3. Covariance functions estimate parameters more efficiently, due to the fact that more data points are used in the analysis.

Calculating the covariance function starts with the classical genetic (co)variance matrix for the traits of interest, often referred to as **G**. Starting with **G**, covariance functions are built by using a smooth

curve to interpolate the values of **G** between the varying ages or points in time (Kirkpatrick et al., 1990; Kirkpatrick et al., 1994: Speidel et al., 2010). Any number of covariate functions can be used, but in general, the covariates used in genetic evaluation of livestock have been restricted to relatively simple polynomial functions that are known to fit the data well (Jensen, 2001). Kirkpatrick et al. (1990) recommended using an orthogonal polynomial function like Legendre polynomials because of their ability to provide smooth curves when linking observations between ***x*** and ***y*** and they have become the most used polynomial functions in livestock genetic evaluation. The procedure to calculate Legendre polynomials was outlined by Speidel et al. (2010) and is as follows:

The polynomials are defined as:

$$P_0(x) = 1 \text{ and } P_1(x) = x$$

Higher order polynomials $P_{n+1}(x)$ are calculated using the following recursive formula:

$$P_{n+1}(x) = 1/n+1[(2n+1)xP_n(x)-nP_{n-1}(x)]$$

Once calculated, these values are normalized using the following equation:

$$\phi_n(x) = \sqrt{2n + \frac{1}{2}}\, P_n(x)$$

Table 2.2 illustrates normalized Legendre polynomials up to a fourth order polynomial using the above equations.

Table 2.2. Normalized Legendre polynomials up to a fourth order polynomial.

Order	Legendre Polynomial	Normalized Legendre Polynomial
n=0	$P_1(x) = x$	$\phi_0(x) = 0.7071$
n=1	$P_2(x) = 3/2x^2 - 1/2$	$\phi_1(x) = 1.2247x$
n=2	$P_3(x) = 5/2x^3 - 9/6x$	$\phi_2(x) = 2.3717x^2 - 0.7906$
n=3	$P_4(x) = 35/8x^4 - 45/12x^2 + 3/8$	$\phi_3(x) = 4.6771x^3 - 2.8062x$
n=4	$P_5(x) = 63/8x^5 - 35/4x^3 + 15/8x$	$\phi_4(x) = 9.2808x^4 - 7.9550x^2 + 0.7955$

Once the Legendre polynomials are normalized, they are then inserted into a matrix Λ such that:

$$\Lambda' = \begin{bmatrix} 0.7071 & 0 & 0 & 0 & 0 \\ 0 & 1.2247 & 0 & 0 & 0 \\ -0.79606 & 0 & 2.3717 & 0 & 0 \\ 0 & -2.8062 & 0 & 4.6771 & 0 \\ 0.7955 & 0 & -7.9550 & 0 & 9.2808 \end{bmatrix}$$

Legendre polynomials are defined over the interval of –1 to 1 (Kirkpatrick et al., 1990), so it is necessary to standardize the ages of the observations to the same interval. The formula for standardized age covariates was presented by Schaeffer (2004) and is defined as follows:

$$t_i^* = -1 + 2\left[\frac{t_i - t_{min}}{t_{max} - t_{min}}\right]$$

where t_i^* represents the standardized time, t_i is the time point being standardized, and t_{min} and t_{max} were the minimum and maximum time points or ages represented in the dataset, respectively. The standardized covariates are placed into a matrix **M**, whose order depends on the maximum number of values of the covariates within the dataset (rows) and the order of the Legendre polynomial implemented (columns). Consider an example of a linear RRM with Legendre polynomials as the base function with an age vector of ten consecutive weeks:

$$t_i' = [1\,2\,3\,4\,5\,6\,7\,8\,9\,10]$$

The standardized ages would be:

$$t_i^* = [-1.0\ -0.778\ -0.556\ -0.333\ -0.111\ 0.111\ 0.333\ 0.556\ 0.778\ 1.0]$$

The first column of the **M** matrix is a column of ones representing the intercept of the curve, whereas the second column corresponds to the standardized ages. The **M** matrix of standardized covariate values would then be:

$$\mathbf{M} = \begin{bmatrix} 1 & -1.000 \\ 1 & -0.778 \\ 1 & -0.556 \\ 1 & -0.333 \\ 1 & -0.111 \\ 1 & 0.111 \\ 1 & 0.333 \\ 1 & 0.556 \\ 1 & 0.778 \\ 1 & 1.000 \end{bmatrix}$$

Fitting higher order polynomials can be accomplished by the addition of columns for the parameters needed in the **M** matrix. The next step is to combine the standardized ages and the Legendre polynomials into a matrix $\Phi = M\Lambda$. Mrode (2014) outlined the steps of calculating Φ in great detail using an example with DIM. Performing this step with the **M** defined above and using a 1st order Legendre polynomial gives the matrix:

$$\Phi = \begin{bmatrix} 1 & -1.000 \\ 1 & -0.778 \\ 1 & -0.556 \\ 1 & -0.333 \\ 1 & -0.111 \\ 1 & 0.111 \\ 1 & 0.333 \\ 1 & 0.556 \\ 1 & 0.778 \\ 1 & 1.000 \end{bmatrix} \begin{bmatrix} 0.7071 & 0 \\ 0 & 1.2247 \end{bmatrix} = \begin{bmatrix} 0.7071 & -1.2247 \\ 0.7071 & -0.9526 \\ 0.7071 & -0.6804 \\ 0.7071 & -0.4083 \\ 0.7071 & -0.1361 \\ 0.7071 & 0.1361 \\ 0.7071 & 0.4083 \\ 0.7071 & 0.6804 \\ 0.7071 & 0.9526 \\ 0.7071 & 1.2247 \end{bmatrix}$$

The values in Φ are the covariate values needed in the incidence matrices relating observations in ***y*** to the fixed and random effects. To produce an estimated coefficient matrix from the which the covariance functions can be used in a RRM we combine Φ with the original genetic (co)variance matrix **G** using the following formula:

$$\hat{C}_G = \Phi^{-1}\hat{G}[\Phi^T]^{-1}$$

The estimated C matrix can be used in conjunction with the following covariance function to estimate covariance between any two measurements taken at any two standardized times denoted as t_1 and t_2 (Kirkpatrick et al., 1990; Kirkpatrick et al., 1994):

$$f(a1, a2) = \sum_{i=0}^{\infty}\sum_{j=0}^{\infty}[C_G]_{ij}\ \Phi_i(t_1^*)\Phi_j(t_2^*)$$

where $[C_G]_{ij}$ is the i[th] and j[th] element of the estimated $\hat{\mathbf{C}}_G$, and $\Phi_{i(j)}$ is the Legendre polynomial coefficient for the i[th] age and j[th] order. However, this equation is limited in use as phenotypic measurements are typically observed at n ages, resulting in only an n [X] n truncated version of $\mathbf{C}_G$ able to be used (Kirkpatrick et al., 1990). Meyer and Hill (1997) indicated that the RRM is equivalent to a covariance function model and this equivalence was shown through an example by Mrode (2014). Regardless, these RRM models and covariance functions allow breeders to obtain estimated breeding values (EBV) for all animals in a population regardless of whether phenotypes of each animal are recorded at all time points with the range of values implemented in the covariance function (Speidel et al., 2010). To obtain a vector of EBV of animal j, including all possible values of the specific covariate used, Oliviera et al. (2019) outlined the following simple equation:

$$EBV_j = \Phi\hat{a}_j$$

where Φ is a matrix of independent covariates for all time points (e.g., all ages) associated with the function used, and $\hat{\mathbf{a}}_j$ is the vector of EBV for the covariance function coefficients of animal j.

The benefit of RRM is rooted in its ability to provide selection tools based on each animal's entire trajectory over a relevant biological performance curve (Kirkpatrick et al. 1990; Meyer, 1998; Meyer and Kirkpatrick, 2005; Stinchcombe et al., 2012). Additionally, RRM methodology has been shown to be effective in evaluating longitudinally measured fertility traits such as cow fertility (Jamrozik et al., 2013; Oliviera et al., 2019). Schaeffer (2004) described how RRM is a useful tool in evaluating fertility traits because reproductive performance can be age dependent and changes over time. Even though HP is recorded as a single-occurrence phenotype of a heifer being able to conceive within a defined breeding season and calve at 2 years of age, HP is still age dependent given its relationship with age at puberty (Speidel et al., 2018b). Due to the ability of RRM to overcome ECP problems, its ability to better incorporate genomic information, and being readily adaptable for use in a multi-breed single-step super

hybrid marker effects model (Golden et al., 2018), RRM has been suggested as an alternative statistical method for the genetic evaluation of HP (Dorian Garrick, personal communication).

Speidel et al. (2018b), provided the first example of a single trait, linear RRM using Legendre polynomials as the base function, prototype for HP genetic evaluation. Since HP observations are observed only once in an animal's lifetime, and no female will have more than 1 HP observation, the authors did not include a block of equations for permanent environmental effects and did not include a non-zero additive genetic covariance between the intercept and linear components of the RRM. Heritabilities for the resulting intercept and linear term (slope) were 0.10±0.01 and 0.10±0.03, respectively, and estimates for the phenotypic and residual variances were estimated to be 0.181±0.0052 and 0.146±0.0014, respectively (Speidel et al., 2018b). The authors then transformed the variance estimates to correspond to an age of 460 days (assumed breeding pasture entrance age), to obtain an observed heritability estimate of 0.09±0.01. This estimate is generally lower than heritability estimates for HP on the underlying scale or estimates commonly used in HP NCE.

Sánchez-Castro et al. (2020) investigated the use of a linear RRM with Legendre polynomials as the base function for the evaluation of first-service conception rate (FSCR) in Angus heifers which was a binary trait defined as the success/failure of a heifer having a fetus of appropriate size relative to AI date. Heritability estimates for the intercept and linear term were 0.002±0.012 and 0.138±0.078 respectively, and the transformed heritability estimate was 0.005±0.001 corresponding to the average age at AI (422d). The authors performed a traditional TM analysis for FSCR on this same population, and reported a heritability estimate of 0.03±0.02. Sánchez -Castro (2021) implemented a similar procedure for the evaluation of HP comparing TM methods, and a linear RRM with Legendre Polynomials as the base function. Heritability estimates were reported as 0.04 on the underlying scale using a TM model, and 0.02 and 0.11 for the intercept and linear term using RRM respectively. Transforming the RRM variance estimates, heritability estimates for HP were displayed across the entire range of age at first exposure (AFE). For the standardized average AFE (422d), the heritability estimates for HP was 0.02, but there were notably higher heritability estimates on the tails of the AFE range. Sánchez -Castro (2021) suggested

the reason for low heritability estimates for both the TM and RRM methods could be due to the extreme phenotypic incidences recorded for the trait across the period of data reporting (1992 to 2019), with high pregnancy frequencies of 90% or higher in many years.

For the above studies, heritability estimates for HP and FSCR using RRM techniques appeared to be reasonable and within ranges reported in literature. Though due to the standardizing function, estimates corresponding to the extremes of the age range were much higher than in the middle, which is consequently where most observations occur. Schaeffer and Jamrozik (2008) suggested that a common problem with RRM using Legendre polynomials as the base function is their tendency to inflate the genetic variances at the beginning and the end of the data age range. This happens because RRM are sensitive to changes in data distribution, especially to reductions in the number of records associated with the implemented covariate (Brugemann et al., 2013). Another common limitation using RRM methods is the selection of the most appropriate mathematical function to fit the data of the performance curve (Mistzal et al., 2000). Legendre polynomials have been extensively used in genetic evaluations because they produce smooth curves akin to those observed in biological phenomena (Kirkpatrick et al., 1990). However, it is important to note their potential limitations, such as higher-order polynomials being "wiggly" and lacking asymptotes (Pletcher and Geyer, 1999). The issue with higher-order polynomials is that the error in a polynomial approximation of a curve increases with the polynomial's order of fit, with errors primarily occurring at the curve's extremes, mathematically known as "Runge's phenomenon" (de Boor, 2001; Meyer, 2005). Speidel et al. (2010) concluded that polynomials place significant emphasis on observations at the extremes, exacerbating the occurrence of Runge's phenomenon. Misztal (2006) also noted that Legendre polynomials have additional issues, such as insufficient information to estimate many parameters and their sensitivity to the numerous different (co) variance parameters.

2.3.3 Linear mixed models

Although heifer fertility traits are generally observed as binary observations, which do not lend themselves well to linear mixed model methods, early investigations into HP tested the utility of linear

mixed models. Henderson (1949) developed a methodology called best linear unbiased prediction (BLUP), so that fixed effects and breeding values can be simultaneously estimated. This method's properties revolutionized animal breeding and genetic selection and is the foundation for all genetic evaluations in the beef industry. The theoretical background of BLUP for a univariate linear animal model will be briefly presented, and as described by Mrode (2014) can be shown in matrix form as:

$$y = Xb + Za + e$$

where ***y*** is a vector of observations, **X** is an incidence matrix relating observations in ***y*** to fixed effects, ***b*** is a vector of fixed effects, Z is an incidence matrix relating observations in ***y*** to random animal effects, ***a*** is a vector of random animal effects, and ***e*** is a vector of random residuals. It is assumed that residual effects, including random environmental and non-additive genetic effects are independently distributed with variance σ_e^2, so that $var(e) = I\sigma_e^2 = R$; $var(a) = A\sigma_a^2 = G$ and $cov(a, e) = cov(e, a) = 0$, where **A** is the numerator relationship matrix. The MME for a univariate linear animal model is then described by Mrode (2014) as:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

when assuming **R** and **G** are non-singular, and $\mathbf{R}^{-1}$ is an identity matrix, it can be factored out from both sides of the above equation to give:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'Y \end{bmatrix}$$

with:

$$\alpha = \frac{\sigma_e^2}{\sigma_a^2} = \frac{(1 - h^2)}{h^2}$$

The assumptions of the above MME, are that distributions in ***y***, ***a***, and ***e*** are assumed to be multivariate normally distributed, the variances for **R** and **G** are known, and the MME can account for selection if based on a linear function of ***y***. The assumption that observations are multivariate normally distributed is what makes linear MME for the evaluation of binary traits like HP problematic. Such traits are likely to have an underlying normal continuous distribution of values but must be scored as a binomial

variable (Van Vleck, 1971). Milagres et al. (1979) presented that cow fertility traits had lower heritability estimates unless binary observations were adjusted to a normal basis according to Van Vleck (1971). Buddenberg et al. (1989) reported that heritability estimates were higher when evaluating HP on the underlying scale than the observed scale. Because binomial data violates the assumptions of normality in the univariate linear animal model, other statistical methods such as TM or RRM are the preferred models for the evaluation of binary fertility traits.

2.3.4 Multi-breed genetic evaluation

An important development to NCE, is that of using composite and crossbred animals as data sources for an expanded multi-breed genetic evaluation. A multi-breed genetic evaluation can drastically increase the number of usable phenotypes for trait evaluations by not relying only on evaluation of purebred or fullblood progeny. Genetic comparisons between breeds are also valuable in development of breeding objectives and strategies for multiple-breed management systems capturing the benefit of heterosis (Arnold et al., 1992). As composites became more popular in beef cattle seedstock populations, models for the evaluation of composite and crossbred animals were developed (Pollack and Quaas, 2005). Robison et al. (1981) were one of the first to present a model for the analysis of direct and maternal additive genetic, and heterotic effects in crossbred dairy data and their approach assumed the following:

1. Observations are linear combinations of breed additive (both direct and maternal) effects and breed combinations (heterosis for direct, paternal and maternal effects).
2. Breed effects are regressed by the fraction of genes represented in an individual for that breed with genes originating from sire or the dam delineated separately.
3. Maternal breed effects are included and regressed by fraction of genes in the dam representing each breed.
4. Heterosis effects for the direct (maternal) expression of a trait due to dominance are regressed by the percentage of loci in the individual (dam) with alleles from different breeds.

The addition of breed and heterosis effects can become computationally challenging with an increasing number of breeds represented in NCE populations. When using MME, including too many fixed and random effects can lead to several issues such as increased model complexity, computing constraints, overfitting, multicollinearity, and difficulty with model interpretation (Harrison et al., 2018). As a result, investigations into grouping strategies for delineating breeds within genetic evaluations were performed. Thompson (1979) described using ancestral group information in a sire model by modifying the structure of the NRM. Westell and Van Vleck (1984) and Westell et al. (1988) presented an alternative method of modifying the MME to incorporate genetic groups such that the solutions of animal equations are genetic evaluations. Though these genetic groups were initially designed to overcome challenges in dairy evaluation, they provided an opportunity to incorporate breed effects into a multi-breed trait evaluation. Arnold et al. (1992) refined the genetic groups strategy for use in a multibreed genetic evaluation for a single-trait animal model by modifying the MME to include a matrix relating breed fractions to individuals in their respective breed groups. The modified MME for breed effect inclusion is presented as:

$$y = Xb + Zu + Wh + e$$

where $\boldsymbol{y}$ is a vector of observations, $\boldsymbol{b}$ is a vector of fixed effects, $\mathbf{X}$ is an incidence matrix relating the fixed effects (e.g. contemporary group) effects of $\boldsymbol{b}$ to the vector of observations in $\boldsymbol{y}$, $\boldsymbol{u}$ is a vector of random additive genetic animal solutions, $\mathbf{Z}$ is an incidence matrix relating the vector of random additive genetic animal solutions to observations in $\boldsymbol{y}$, $\boldsymbol{h}$ is a vector of nonadditive effects (e.g. heterosis), $\mathbf{W}$ is an incidence matrix relating the nonadditive effects in $\boldsymbol{h}$ to observations in $\boldsymbol{y}$, and $\boldsymbol{e}$ is a vector of random residual effects. A modification was introduced to more precisely partition $\boldsymbol{u}$ into fixed and random components (Quaas and Pollak, 1981). Following this logic, $\boldsymbol{u}$ may be expressed as:

$$u = Qg + a$$

where $\mathbf{Q}$ is a matrix relating fractions of breed group effects to the animal, with these fractional contributions proportional to the breed composition of the animal, $\boldsymbol{g}$ is a vector of fixed additive breed group effects, and $\boldsymbol{a}$ is a vector of random additive genetic effects. With this modification, animals of

mixed-breed ancestry receive a linear combination of breed-group effects proportional to their breed composition. Similarly, the nonadditive genetic (heterosis) effects contained in h will also be partitioned into fixed and random components expressed as:

$$h = Sd + T\delta$$

where **S** is a known incidence matrix relating the vector of fixed heterosis effects represented in ***d*** to parents of the individual making the record, and **T** is an incidence matrix relating the vector of random heterosis effects represented in δ to the vector of observations. The vector of fixed heterosis effects represents the fixed effects of particular sire breed x dam interaction. This model modification has become the foundation for all current multi-breed genetic evaluations.

Rodriguez-Almeida et al. (1997) tested the application of this methodology across three populations of Meat Animal Research Center (MARC) composite breeds (MARC I, II, and III). The results from their analysis produced distinctly different estimates of direct and maternal breed effects for Hereford, Simmental, and Gelbvieh influence. However, the authors summarized the separation of direct and maternal breed effects requires data from a variety of breed crosses which could present challenges in populations with unequal breed crossing. Klei et al. (1996) proposed using a Bayesian approach that uses an appropriate model for the analysis of multi-breed information, combining prior literature estimates of breed and heterosis effects with pooled data to provide across-breed genetic values. In breed association populations, where animals of varying breed combinations are present, this methodology can effectively be applied. The American Simmental Association has leveraged this methodology for their genetic evaluation since 1997 (Wade Shafer, personal communication). In the absence of populations with varying breed combinations, and no prior literature, estimates for breed effects and heterosis must be derived. Legarra et al. (2007) investigated different analysis for the evaluation of growth traits in a multibreed Gelbvieh population by varying the weights of literature and derived breed effects, heterosis, and breed-of-founder (BOF) x generation group effects. They reported large difference were observed for heterosis estimates, BOF x generation estimates, and the EBV due to weights varying from literature

estimates and those that were derived; however, the rankings within breed were relatively robust to the different weights.

Arnold et al. (1992) alluded to the importance of correctly identifying breeds represented in individuals as their evaluation is a function of their breed effects. As breed associations have developed "breeding-up" programs to elevate animals from composite ancestors to purebred status, incorrect breed fractions can be represented. Traditional methods of breed identification use fractional representation (e.g., 1/2 Simmental, 1/2 Angus), which are becoming increasingly inadequate as composite cattle populations interbreed over multiple generations. Most fractions are limited to increments of 1/32, which introduces rounding errors that can misclassify animals as purebred in a breeding-up program when they still possess significant contributions from other breeds. Expressing breed composition as continuous breed proportions with values ranging from 0 to 1 (e.g., 0.51 Simmental, 0.49 Angus) allows for a more accurate depiction of genetic breed makeup, mitigating these inaccuracies.

Additionally, multi-breed evaluations may also rely on the evaluations of animals from other breed associations which are not present in the NCE. Pollak and Quaas (2005) present an example of prolific Angus bulls used as sires in the American Simmental Association (ASA) and Canadian Simmental Association (CSA) registries, where the evaluations of the same sires in the Angus genetic evaluation would differ substantially in the ASA and CSA evaluations. A solution was presented by Quaas and Zhang (2001), that incorporated the animals "external EPD" from the Angus evaluation as starting values in the joint ASA-CSA genetic evaluation. Using external EPD from foundation sires in multi-breed genetic evaluations typically results in more similar genetic predictions for the same sire across both evaluations and higher prediction accuracy for the sire in the external evaluation (Quaas and Zhang, 2006).

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CHAPTER 3 - WHOLE HERD REPORTING DATA FROM THE AMERICAN SIMMENTAL ASSOCIATION AS A DATA SOURCE FOR HEIFER PREGNANCY PHENOTYPES

Summary

Replacement female fertility represents a primary influence on the profitability of a cow-calf enterprise. Selection for improved reproductive performance in replacement heifers has proved difficult due to the influence of multiple, extraneous factors and the lack of phenotypic data needed to establish a reliable genetic prediction. Presently, few beef cattle breed associations have a genetic prediction for heifer reproductive performance. The goal of this study was to evaluate whole herd reporting (WHR) productivity and disposal information from the American Simmental Association (ASA) as a source for establishing heifer pregnancy (HP) phenotypes in a multi-breed genetic evaluation of heifer pregnancy. Observations for HP were coded as 1 or 0 for heifer exposure (EXP = yes or no), 1 or 0 for heifer pregnancy success (BRED = yes or no). Data were provided by the ASA on 400,469 animals with complete WHR information since 2009 for the assignment of HP phenotypes. Heifers whose birth year plus 2 years of age and included on preliminary ASA WHR inventory were included. Out of the 400,460 females, a total of 240,861 heifers were subsequently enrolled in WHR inventory, where 203,173 females were determined to have a successful EXP observation and known BRED observation. A total of 159,608 heifers were disposed and not kept on WHR inventory at ASA; however, 19,976 were determined to have a successful EXP observation and known BRED observation. A total of 223,614 heifers since 2009 were assigned a successful EXP observation, where 31,816 females were identified as having an unsuccessful observation for BRED. This indicated 14% of the Simmental heifer population since 2009 experienced reproductive failures, consistent with the national average of heifer infertility in the United States, indicating WHR information may provide more accessible data for development of a HP genetic prediction.

3.1 Introduction

Reproductive rates in young females determine the amount of calf product sold at weaning in beef production systems and thus is a primary contributor to the financial success of commercial cow-calf enterprises. Commercial producers also risk losing initial investments in the developmental costs of young females who do not breed and stay pregnant. At the seedstock level, genetic progress can be slowed with poor AI conception rates and replacement heifer breeding rates, resulting in reduced selection intensity and generation interval. Heifer pregnancy expected progeny differences (EPD) estimate the differences among individuals in the proportion of their daughters that will successfully conceive to calve at 2 yr of age (BIF Guidelines, 2021). Research suggests that heifer pregnancy (HP) is a moderately heritable trait with estimates ranging from 0.14 to 0.53 (Evans et al., 1999; Van Melis et al., 2010; McAllister et al., 2011). However, genetic progress for fertility traits in beef cattle has been slowed by low to moderate heritability of reproductive efficiency traits and a lack of reliable field data.

Phenotypic data for HP in the form of a heifer exposure inventory include breeding start and end dates, individual exposure status, management group, breeding pasture, disposal information, individual bred status, and a yearling weight contemporary group definition. Additional useful HP information could also include artificial insemination (AI) service dates, AI sire identification, AI protocol, observed natural service, and pregnancy results (BIF Guidelines, 2021). Phenotypic pregnancy observations have been difficult to collect among the major beef cattle breed associations (Speidel et al., 2018). Scrotal circumference (SC) as an indicator trait for HP has been investigated to help improve predictions where HP data are scarce (Evans et al., 1999); however, few genetic evaluations have implemented this methodology and have instead developed standalone genetic predictions for SC. Some breed associations have developed a HP prediction under the assumption that a heifer with a yearling weight observation is assumed to have been exposed and those that report a calf at 2 yr of age were successfully bred to overcome the lack of HP inventory observations (Speidel and Enns, 2015).

Inventory-based whole herd reporting (WHR) has been suggested as an enticing source of information on a range of economically relevant traits, notably reproductive efficiency traits (Hough and

Ponder, 2001; Cammack et al., 2009). Whole herd reporting is the collection and reporting of production information on every cow and the performance data of every calf raised through weaning in a production system. The benefits of WHR include the calculation of unbiased growth predictions in addition to the collection of reproductive performance data on entire female contemporaries in a production system. Industry adoption of WHR processes in breed association registry services was historically slow among U.S. breed associations since it was first proposed in the late 1990s. However, many breed associations now offer robust WHR programs, and several organizations even require mandatory WHR from members to take advantage of the unbiased growth predictions and ability to predict EPD for traits like Stayability (Krymowski, 2019). These reporting programs for breed associations accumulate many productivity and disposal information that are predominantly unused within National Cattle Evaluations (NCE) today. These productivity and disposal codes provide an opportunity to understand specific reasons animals leave a herd early and what proportion issues such as infertility, structural soundness, or udder failure are prevalent in a breed-specific population. The objective of this study was to identify the merit of using WHR productivity and disposal information as a data source to establish heifer pregnancy phenotypes when heifer inventory data were not reported.

3.2 Materials and Methods

Data used in this study were obtained from an existing database, and as such, an Institutional Animal Care and Use Committee (IACUC) approval was not required.

3.2.1 Data description

Presently, there are no standard practices for the implementation and use of WHR data in the beef industry. Many WHR programs lack precise descriptions of productivity and disposal reasoning, with few organizations enforcing WHR data submission compliance. The data used in this study were a subset of a larger HP dataset (n = 740,423) provided by International Genetic Solutions (IGS), where data from American Simmental Association (ASA) females enrolled in the Total Herd Enrollment (THE) inventory-reporting program were queried. Females were first eligible to be on THE inventory when they turned 2

years of age, so females whose birth year plus 2 years were included in this study (n = 400,469). The ASA did not have an avenue for members to submit heifer inventory information such as heifer exposure, breeding dates, or breeding pasture data. Using THE status, productivity codes, and evaluating enrollment status, a methodology was developed to assign heifer exposure (EXP) and bred status (BRED) phenotypes. A list of THE enrollment, productivity, and disposal codes and descriptions can be found in Tables 3.1 through 3.3.

All females approaching 2 years of age were automatically included on an ASA member's preliminary inventory every year/season. Spring herds were classified as dams that will calve between January 1 and June 30 of a given year. Fall herds were classified as dams that will calve between July 1 and December 31 of a given year. Heifers that stayed on a member's inventory must have had an enrollment status code indicating her status and intent to stay in the herd (Table 3.1). Heifers that did not stay on a member's preliminary inventory must have a disposal status code indicating her reason for leaving the herd (Table 3.3). Enrolled heifers that stay on a member's inventory the following year must have a productivity status code (Table 3.2), and females that left an inventory after a year must have a disposal status code (Table 3.3).

Table 3.1. Code and description of American Simmental Association Total Herd Enrollment heifer enrollment codes.

Enrollment Code	Description
0	Cow bred to calve during season
1	Heifer bred to calve during the season
2	Not exposed – moved to next season
3	Exposed and failed to conceive – moved to the next season
4	Exposed and failed to conceive – moved to next year
5	Embryo transfer donor
6	Embryo transfer recipient
44	Not exposed – moved to next year

Table 3.2. Code and description of American Simmental Association Total Herd Enrollment heifer productivity codes.

Productivity Code	Description
1	Calf/calves stillborn
2	Aborted
3	Not exposed to calve in given season/year
4	Cow calved
5	Embryo transfer donor
6	Embryo transfer recipient
7	Exposed and failed to conceive – moved to next season
8	Exposed and failed to conceive – moved to next year
9	Exposed and failed to conceive – removed from the herd
10	Calving interval overlaps season (Dec-Jan; Jun-Jul)
11	Bred – but sold, removed or died prior to calving
12	Cow calved – calf not found intact or at all

In some cases, animals that have an initial inventory disposal status code were also given a productivity code. Users were able to assign up to 2 disposal codes per dam, with the first being a "primary code" and the second being an "additional code." Only primary disposal codes were evaluated in this study. Each code combination was evaluated to establish a heifer pregnancy record satisfying: 1) whether a female on enrollment was exposed and given the opportunity to become pregnant (EXP = yes or no), and 2) whether a female was successfully bred or failed to conceive (BRED = yes or no). The default for both EXP and bred status BRED was n = no.

Table 3.3. Code and description of American Simmental Association Total Herd Enrollment heifer disposal codes.

Disposal Code	Description
60	Exposed and failed to conceive
61	Aborted
62	Age
63	Appearance
64	Calf loss at calving
65	Calf loss post calving
66	Color
67	Died - calving
68	Died - other
69	Died – sickness/disease
70	Disposition
71	Herd reduction
72	Hoof condition
73	Horned
74	Injury
75	Production/performance
76	Prolapse
77	Sickness/disease
78	Sold, breeding purposes, paper not transferred
79	Sold, breeding purposes, paper transferred
80	Structural soundness
81	Udder quality
82	Genetic defect status

Data on THE females were only included on animals born in 2009 or after since ASA THE processes were not enforced for compliance prior to 2009. Compliance was a process established in 2009 to ensure timely data submission and accurate reporting of dams among THE herds. Participants were required to provide either a disposal code or productivity code for dams on inventory by the deadline (spring = February 15, fall = August 15) for each season enrollment. When a disposal or productivity code was not provided for a dam on inventory, participants were considered "non-compliant," and no transactions could be processed until a status code was provided, and females were given a late enrollment fee. Participants' enrollment for ASA spring THE opened from October 15 to December 15,

and productivity/disposal codes on enrolled females were regularly reported the following April through October, indicating that there was a 5- to 10-mo delay in productivity/disposal code reporting on enrolled females.

3.3 Results and Discussion

The assignment of EXP and BRED phenotypes on THE females was determined using both the status and productivity codes. A total of 400,469 THE heifers were enrolled or disposed of since 2009. Data counts for EXP and BRED designations are provided in Table 3.4. All females given a 0, 2, 5, 6, or 44 enrollment code were removed from this dataset and given an unsuccessful EXP observation as a heifer.

Table 3.4. Designation counts of American Simmental Association Total Herd Enrollment (THE) females for enrollment and exposed status.

Designation	Count
Total number of THE heifers since 2009	400,469
Total number of heifers enrolled since 2009	240,861
Total number of heifers not enrolled since 2009	159,608
Number of heifers not enrolled and not exposed	139,632
Number of heifers not enrolled but exposed	19,976
Number of heifers enrolled and exposed	203,173
Number of heifers enrolled but not exposed	37,688
Number of heifers exposed and with a bred status	223,149
Number of heifers enrolled but without productivity – herd dropout	16,603

Females that were enrolled in THE inventory (n = 240,861) had 71 unique enrollment and productivity code combinations. The largest category of heifers that received a successful observation for EXP and BRED came from those that had an enrollment code of 1 and a productivity code of 4, identifying those females that were enrolled on inventory as a heifer bred to calve during the season of enrollment and successfully calved (n = 176,534). Heifers that received an enrollment code of 1 and productivity codes of 1, 2, 4, 7, 8, 9, 10, 11, or 12 were given a successful EXP observation, but only

heifers receiving productivity of 1, 2, 4, 11, or 12 were assigned a successful BRED observation. There were 9,017 females that were exposed but failed to conceive (productivity = 7, 8, or 9) if being enrolled as a 1. A small portion of females were sold as bred (n = 10,554), and some were reported to have aborted, had a stillborn, or calved, but no calf was found (n = 1,484, 1,220, and 761, respectively). Heifers that received an enrollment code of 3 or 4 were assigned a successful EXP observation, but an unsuccessful BRED observation (n = 3,207). A total of 223,149 heifers were assigned a successful EXP observation and a known BRED observation among this group.

The primary reasons for heifer disposal are described in Table 3.5. The majority of heifer inventory disposals were from selling open/bred heifers or herd reduction, reflecting 62% of all heifer disposals. There was a large percentage of females sold with registration certifications transferred, possibly opening the opportunity for an additional population to be evaluated for an HP phenotype assignment. However, determining the enterprise where breeding took place may be difficult to identify without additional investigation or added tracking on those females sold with registration certifications transferred. The production or performance of young stock was also evaluated, and the cause for removal reflected 13% of heifer disposals. This is encouraging, suggesting that many producers participating in THE are using performance predictions in their culling decisions compared to culling based on appearance, which reflects 7% of heifer disposals.

Table 3.5. Percentage of disposal reasons among American Simmental Association Total Herd Enrollment (THE) heifers since 2009.

Disposal Code	Description	Record count	Percentage of disposals
60	Exposed and failed to conceive	19,163	12.0%
61	Aborted	410	0.3%
62	Age	482	0.3%
63	Appearance	11,708	7.3%
64	Calf loss at calving	165	0.1%
65	Calf loss post calving	121	0.1%
66	Color	268	0.2%
67	Died - calving	117	0.1%
68	Died - other	2,599	1.6%
69	Died – sickness/disease	675	0.4%
70	Disposition	2,570	1.6%
71	Herd reduction	41,158	25.8%
72	Hoof condition	332	0.2%
73	Horned	54	0.0%
74	Injury	394	0.2%
75	Production/performance	20,279	12.7%
76	Prolapse	99	0.1%
77	Sickness/disease	238	0.1%
78	Sold, breeding purposes, paper not transferred	40,640	25.5%
79	Sold, breeding purposes, paper transferred	17,431	10.9%
80	Structural soundness	504	0.3%
81	Udder quality	27	0.0%
82	Genetic defect status	174	0.1%

Females who were removed from inventory and not given an initial enrollment code were assigned successful and unsuccessful EXP and BRED observations based on their disposal and productivity codes. In practice, females who were removed from THE should not have received a subsequent productivity code; however, in some cases, both are identified. There were 80 unique combinations of female groups that were reported with a disposal code and a productivity code. All females with disposal codes apart from 60, 61, 64, 65, and 67 were removed from this dataset and assigned an unsuccessful EXP and BRED status, regardless of if a subsequent productivity code could identify a female had calved successfully. Since productivity code reporting timeframes vary, there is not

a great way to track whether the female was given the opportunity to become pregnant in a given enrollment season nor given the opportunity to become pregnant among her contemporaries. Females that received a disposal code of 60, regardless of productivity, were assigned a successful EXP observation and an unsuccessful BRED observation (n = 19,163). Females that either aborted, lost a calf at birth, or died in calving and were removed from the herd for these reasons were included in this dataset. Females receiving disposal codes 61, 64, 65, or 67 were all assigned successful observations for EXP and BRED (n = 813).

A total of 31,816 females were identified since 2009 as having had the opportunity to become pregnant but failed to succeed in that pregnancy. The percentage of reproductive failures within this population of Simmental heifers was 14%. This proportion is consistent with the national average found in 2017, where the National Animal Health Monitoring System evaluated data across 24 of the major U.S. cow-calf states and reported 83% of heifers and 94% of cows calved when given the opportunity to become pregnant in 2017 (USDA, 2020). It appears this methodology of assigning HP phenotypes from WHR codes appropriately identified reproductive efficiencies consistent with the national beef cattle average and could be a useful tool for breed associations to capture HP data when heifer inventory data were not reported. Prevatt et al. (2018) found that a reduction of 2% in reproductive infertilities could reduce economic loss by $1,800 per 100 head annually for a beef cattle enterprise.

3.4 Implications

Whole herd reporting appears to provide sufficient data for the development of a heifer pregnancy EPD as a selection tool to improve genetic merit of fertility and reproductive fitness in replacement heifers. Further investigation into the effectiveness of WHR and the application of records is needed before NCE EPD can be provided to Simmental breeders.

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CHAPTER 4 - COMPARISON OF LINEAR MODELS AND THRESHOLD MODELS FOR THE GENETIC EVALUATION OF HEIFER PREGNANCY IN A MULTI-BREED POPULATION OF BEEF HEIFERS

Summary

Fertility rates are the most economically important trait relevant to beef production, as reproductive rates are responsible for the amount of beef produced. Reproduction's importance is heightened in replacement heifers as producers will have spent a considerable investment in developmental costs for heifers to reach puberty, conceive, and have a live calf before any profits can be made. Unlike the dairy industry, the beef industry has not seen a major decrease in fertility due to the antagonistic selection of other performance traits. However, it is imperative for beef producers to be proactive in maintaining appropriate selection on fertility as it is an economically relevant trait and to ensure future degradation in genetics of fertility do not occur. Traditional genetic evaluation of heifer pregnancy (HP) involves the use of threshold models (TM) that convert a categorical observation (1 = pregnant; 0 = not pregnant) to an underlying, normally, distributed range of values known as liabilities. These methods have been deployed for HP genetic evaluations at the American Angus Association, and the Red Angus Association of America. However, using TM methods for evaluating HP has not led to major improvements in genetic trends across the industry. This is most likely due to the general apathy of beef producers towards the trait that they would rather select for improved growth or terminal merit. But another reason could be explained by some of the inherent shortcomings of the TM evaluation method, of which their susceptibility to the extreme category problem (ECP) limits the ability to use all available information for genetic evaluation. The case of ECP happens when all observations within a contemporary group are successful (or not), which is common with categorical observations. Additionally, TM are not adapted for use in the BOLT single-step genomic evaluation software programs, limiting their use for organizations that rely on that software to perform national cattle evaluation (NCE).

As breed associations and registry databases have consolidated in recent years, the evolution of multi-breed and global genetic evaluations have necessitated the need to also better understand the impact that heterosis and breed differences have on HP. As such, the objective of this study was to compare linear model (LM) and TM methods for the evaluation of HP and provide an understanding of breed effects and heterosis for multi-breed genetic evaluation. This study used HP data from 1974 to 2020, obtained from the International Genetic Solutions (IGS) database, as well as a HP dataset obtained directly from the Red Angus Association of America (RAAA). Data were reported to IGS by independent breed associations via a secure file transfer portal to a multi-breed database, and there were 9 North American breed associations reporting HP for this study. Observations included binary exposure, binary pregnancy, and heifer management group data. Traditional HP evaluations using LM and TM methods were performed across breed populations with stepwise inclusion of breed and heterosis effects in the model. Variance components and fixed effect solutions were obtained using competing univariate BLUP linear animal models and univariate BLUP threshold animal models. The average heritability estimate across evaluations performed on 7 different breed groups for HP using LM methods was 0.026, with a minimum value of 0 and a maximum of 0.084. The average heritability for HP using TM methods was 0.17, with a minimum of 0.07 and a maximum of 0.28. Breed populations were then combined into a single multi-breed population, and the same stepwise procedure of incorporating heterosis and breed effects as fixed effects was used to generate variance components and fixed effect solutions. The heritability estimates in this multi-breed population were 0.023 and 0.088 using LM and TM methods, respectively. Heritability estimates did not change as additional fixed effects of breed and heterosis were fit. There were no statistically meaningful breed effects; however, heterosis resulted in a 17.2% increase ($P<0.05$) in the probability of HP when maximum heterosis is achieved. As expected in all populations, yearling age was a significant factor affecting HP and resulted in a 0.02% increase ($P<0.05$) in HP probability with each increasing day of yearling age. A series of cross-validation procedures were performed to compare LM and TM evaluation methods. Results from this statistical method suggested that LM and TM may be performing equivalently for estimating HP breeding values in within-breed populations; however, in a

multi-breed population, results were inconsistent, suggesting perhaps the model was over-specified with breed effects. These results suggest that LM may be an alternative evaluation method for HP for within breed evaluations due to its simplicity, ability to use all available information, and support in modern genetic evaluation software programs. However, further evaluation of LM for use in a multi-breed HP genetic evaluation is still required.

4.1 Introduction

Replacement heifer fertility represents a primary influence on the profitability of cow/calf enterprises. Reproductive rates determine the amount of beef produced at the commercial level and, therefore, drive resulting income. Commercial producers also risk losing investment in the development of yearling heifers that do not breed (Clark et al., 2005). A primary concern is the cost of developing heifers to reach an appropriate body weight prior to breeding, and heifers that fail to conceive consume feed resources without providing income (French et al., 2013; Sterry and Halfman, 2020) other than as the sale of a non-pregnant animal. For this reason, placing adequate selection pressure on improved genetics of fertility is necessary for cow/calf operators. Heifer pregnancy (HP) is traditionally defined as the binary observation of a heifer conceiving and remaining pregnant to palpation, given that she was exposed during the breeding season (Doyle et al., 2000). Despite HP being lowly heritable, there is enough genetic variability in most cattle populations to make meaningful genetic improvement (Mackinnon et al., 1990; Doyle et al., 2000; Cammack et al., 2009), though observed genetic trends at the Red Angus Association of America and the American Angus Association have not indicated meaningful improvements (RAAA, 2024; AAA, 2024).

Traditional genetic evaluations for heifer pregnancy (HP) involve the use of threshold models (TM) that convert categorical phenotypes to an underlying normally distributed range of genotypic values known as liabilities (Sánchez-Castro et al., 2020). Categorical responses (e.g., 1 = pregnant, 0 = nonpregnant) violate assumptions of normality and do not possess homogenous variance (Gianola, 1982). The threshold model introduced by Wright (1934) can be used to model discrete variables because it

assumes there is an underlying continuous, unobservable and a normally distributed trait (liability), which becomes discrete (observed scale) when an animal exceeds a particular threshold level for the underlying trait (Falconer and Mackay, 1996). This assumption enables the use of non-linear systems of equations that can predict breeding values, making TM the preferred method for routine genetic evaluations of categorical traits (Foulley, 1992; Gianola and Rosa, 2015). Genetic evaluations based on TM analysis have given a larger rate of response to selection than those based on linear models (Meijering and Gianola, 1985; Misztal et al., 1989). However, computing difficulties have impaired the potential advantage of TM, and a slow or lack of convergence occurs when all responses for a given class of a fixed factor occur in an extreme category (Misztal et al., 1989). As computing power has improved in recent years, the more pressing concern for TM is situations with an extreme case problem (ECP), exhibited when observations for a fixed effect all fall into the same category (e.g., all observations of 0 or 1). This presents poor convergence criteria as such classes tend to gravitate towards $\pm \infty$ or 0 convergence criterion as iteration proceeds (Misztal et al., 1989). Furthermore, TM are not readily adaptable to the incorporation of genomic information in modern single-step genetic evaluations (Speidel et al., 2018) unless genomic relationship matrices are used as seen in the single-step genomic BLUP (ssGBLUP) method (Legarra et al., 2009). In addition, TM have not been adapted into the framework of the super hybrid marker effects models (Fernando et al., 2016), which many beef cattle breed associations use for genetic evaluation.

Some evidence suggests that only small differences in genetic prediction are noticed between TM and linear models (Meijering and Gianola, 1985; Weller et al., 1988; Hagger and Hofer, 1989), suggesting that linear models (LM) could be a useful alternative for the prediction of HP. Parallel to this development, traditional HP genetic evaluations have been limited to within-breed genetic evaluations. The use of composite and crossbred animals in modern seedstock breeding programs has expanded the opportunities for genetic improvement to include multiple breeds in a single genetic evaluation. A multi-breed genetic evaluation can drastically increase the number of usable phenotypes for trait evaluations by not discriminating only on evaluating purebred or full-blood progeny. A multi-breed genetic evaluation

requires the knowledge of breed and heterosis effects for each trait evaluated (Westell et al., 1988) or estimable from the data as well. As such, the objectives of this study were to 1) develop genetic parameter estimates of HP, 2) investigate breed and heterosis effects of HP, and 3) perform a comparison of LM and TM methods for the prediction of HP in a multi-breed population of beef heifers.

4.2 Materials and Methods

Data used in this study were obtained from an existing database, and as such, an Institutional Animal Care and Use Committee (IACUC) approval was not required.

4.2.1 Data collection and description

Data were obtained from a historical database from the American Simmental Association (ASA) and International Genetic Solutions (IGS) genetic evaluation. The IGS genetic evaluation combines data from over 20 beef breed associations globally into a single multi-breed genetic evaluation. As of the writing of this manuscript, there are no genetic prediction tools for heifer fertility traits in the IGS multi-breed genetic evaluation. Heifer exposure and pregnancy data (n=740,423) were retrieved in February 2021 from IGS. There were 9 beef breed associations contributing heifer exposure (1 = Exposed; 0 = Not exposed), pregnancy outcome (1 = pregnant; 0 = not pregnant), and a heifer breeding pasture contemporary group identifier for this study (Table 4.1). It is worth acknowledging, that each breed organization may have its own nuanced definition of HP or differences in how fertility data are reported, and for this reason, inconsistencies in HP data definition need to be investigated. For example, the American Simmental Association (ASA) does not have an upload format for producers to report HP data but instead uses a system of logic converting whole herd reporting (WHR) codes into HP phenotypes. Comparing results across breed populations can serve as a diagnostic tool to identify potential discrepancies in data reporting practices, or varying trait definitions among organizations.

In addition to the heifer pregnancy data file, a performance data file including animal ID, breeder ID, herd ID, birth code, birth contemporary group, weaning management, weaning pasture, weaning contemporary group, yearling feed unit, yearling, contemporary group, serial birth date, serial weaning

date, serial yearling date, birth weight, weaning weight, yearling weight, age of dam, sex, and calving ease code were retrieved on all animals and progeny in the study. Heifers were required to have a successful heifer exposure code (Yes = 1) to be included in the study.

Because numerous breed registries contributed data to this study, there was little to no awareness of breeding season length within contemporary groups (CG) as some breed registries do not require those records to be reported. The Red Angus Association of America (RAAA) uses only producer-reported HP records from breeding seasons equal to or less than 90 d. The American Gelbvieh Association (AGA) has no restrictions on breeding season length. Instead, it uses yearling weight observations to assume a heifer was exposed, and then if a calf out of a heifer is then recorded at around 2 years of age, she will have a successful HP record. The American Simmental Association (ASA) does not accept any producer-reported HP phenotypes but rather relies on a system of converting whole herd reporting (WHR) codes to assign HP phenotypes based on a combination of enrollment, productivity, and culling observations described in Chapter 3. These differences in HP trait definition add additional challenges in developing a multi-breed HP genetic evaluation.

Table 4.1. Heifer exposure and pregnancy data counts submitted by individual beef breed associations.

Breed Association (ICAR ID Prefix)*	Records
Canadian Shorthorn (BSHCAN)	695
American Shorthorn (BSHUSA)	4,660
American Chianina (CIAUSA)	34
Canadian Gelbvieh (GVHCAN)	8,347
American Gelbvieh (GVHUSA)	117,282
Canadian Limousin (LIMCAN)	19,616
American Limousin (LIMUSA)	246,506
American Red Angus (RANUSA)	120,134
American Simmental (SIMUSA)**	223,149
Total	**740,423**

* Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022).
** Data were created from whole herd reporting codes using a process outlined in Chapter 3 of this dissertation.

Contemporary group was defined as a concatenation of breeder ID, herd ID, birth year, birth contemporary group, weaning contemporary group, yearling contemporary group, and heifer pregnancy management group. Red Angus heifers were the only animals with a heifer pregnancy management group observation as they are the only association requiring that information. Heifers with a yearling weight age younger than 200 d and older than 500 d were removed from the study. Records from single-animal contemporary groups and CG with no variation were removed from the study. Breed populations were separated into independent groups, defined by their International Committee for Animal Recording (ICAR) breed and country designation. A more in-depth description of ICAR identifiers is presented in Appendix A. To establish a baseline understanding of HP genetic control in the various breed populations, individual models were applied within breed population before combined multi-breed population models were performed. As a result, numerous populations were used in this study.

4.2.2 Fixed and random effects

There are a variety of important factors impacting HP, notably differences in age, heterosis, and breed effects. The relevant effects influencing HP genetic evaluations have been outlined within the Beef

Improvement Federation's guidelines (BIF, 2020). To determine the significance of proposed factors, incremental Wald F-tests were conducted simultaneously with variance component estimation using Equation 4.1 below:

$$W = [\hat{\theta} - \theta]^{-1} [Var(\hat{\theta})]^{-1} [\hat{\theta} - \theta] \quad \text{Eq. 4.1}$$

where $\hat{\theta}$ represents the maximizing argument of an unconstrained likelihood function, or the maximum likelihood estimate obtained when all potential explanatory variables were included in the model. "Var" denotes the variance, and θ corresponds to the hypothesized maximum likelihood estimate under the assumption that the null hypothesis is true (H_0: $\theta_k = 0$), which assumes that the k_{th} parameter does not help to explain variation in the response variable. The incremental Wald F-test (F-Inc) statistics have an asymptotic X^2 distribution with degrees of freedom given by the number of estimable effects (n-k) that are adjusted using the Kenward-Roger method (Kenward and Roger, 1997). The F-Inc tests the additional variation explained when additional covariates are included and are computed from an incremental sum of squares used in classical regression analysis. For balanced designs, the Wald F-statistics are numerically identical to F-statistics obtained from standard analysis of variance. Denominator degrees of freedom (DenDF) are calculated by ignoring the fixed/boundary/singular variance parameters using numerical derivatives.

Since many heifers with HP phenotypes were registered with their respective breed associations, many females had a yearling weight and yearling age observation. Yearling age (YAGE) was defined as the difference in days between a heifer's birth date and her age when a yearling weight observation was taken. Several models were constructed, with some models restricting the dataset to only those animals that had a recorded yearling weight observation. In contrast, other models allowed for the inclusion of animals with missing yearling age data.

With 9 breed associations contributing data to this multi-breed study and numerous composites representing many breeds in each population, breed differences were investigated as important factors influencing HP. The pedigree file retrieved from IGS contained individual breed proportions for

Simmental, Angus, Hereford, Brahman/Zebu, Gelbvieh, Limousin, Chianina, Maine-Anjou, Shorthorn, Red Angus, Salers, South Devon, Charolais, Holstein, Jersey, Other American, Other British, Other Continental, Other Dairy, and Other or Unknown. Breed groups were consolidated to avoid overfitting the model. As a result, all dairy breeds were combined into a single breed proportion (DAIRY), all *Bos indicus* influenced animals were combined (IND), Salers, Charolais, Maine-Anjou, and Other Continental were combined (CONT), and South Devon, Hereford, Shorthorn, Other Unknown (UNK) and Other English were combined (ENGL). In the present study, there was very little IND representation, and animals with IND >0 were removed from the study. This resulted in breed categories of Simmental (SIM), Black Angus (AAN), Gelbvieh (GBV), Limousin (LIM), Red Angus (RAN), DAIRY, CONT, ENGL, and UNK. Breed proportions were fit as fixed effects, which is generally not the method used in most published similar analyses (Kennedy, 1991), where most methods use ordinary least squares (OLS) to determine breed and cross effects. Henderson (1977), however, recommended estimating breed differences through mixed model equations (MME) with those fit as a fixed effect for estimating specific solutions. Estimating specific effects for the various breed groups is important for obtaining coefficients to assign genetic groups, as described by Westell et al. (1988).

Because there was a diverse breed and composite representation in this study, heterosis was investigated as an influential effect on HP. Since breed proportions of sires and dams were known, the proportion of individual retained hybrid vigor (RHV) was used as an estimate of the degree of heterosis in individual animals and is expressed as a value ranging from 0 to 1. The formula used to estimate RHV was derived from the set of equations presented by Bourdon (2000) and is outlined in equation 4.2 below:

$$\widehat{RHV} = (1 - \sum_{i=1}^{n} p_{s_i} p_{d_i}) \qquad \text{Eq. 4.2}$$

where p_{si} is the proportion of breed *i* in the sires, p_{di} is the proportion of breed *i* in the dams and n is the total number of breeds involved. In expanded form, the formula appears as:

$$\widehat{RHV} = (1 - (p_{s_1}p_{d_1} + p_{s_2}p_{d_2} + p_{s_3}p_{d_3} + \cdots + p_{s_n}p_{d_n}))$$

4.2.3 Animal models for heifer pregnancy evaluation

In this comparative study, numerous linear continuous animal models and threshold models were applied across various breed populations. Historically, genetic evaluations for the prediction of HP have been performed using a univariate BLUP animal threshold model (TM) using a probit link function to convert binary observations to an underlying normal distribution. The model equation for a TM in matrix form (Eq. 4.3) was:

$$y^* = Xb + Zu + e \quad \text{Eq. 4.3}$$

where $\boldsymbol{y^*}$ corresponded to a vector of transformed HP observations on the underlying scale, $\boldsymbol{b}$ was a vector of unknown solutions for fixed effects that included CG, YAGE, RHV, and breed proportions, $\boldsymbol{u}$ corresponded to a vector of unknown random additive genetic solutions of animal random effects. $\boldsymbol{X}$ and $\boldsymbol{Z}$ were known incidence matrices relating observations in $\boldsymbol{y^*}$ to fixed effects in $\boldsymbol{b}$ and random effects in $\boldsymbol{u}$, and $\boldsymbol{e}$ was a vector of unknown residual errors. Random effects were assumed to have a mean of 0 and variances equal to:

$$var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

where **A** was Wright's numerator relationship matrix, and $\boldsymbol{I}$ was an identity matrix with an order equal to the number of observations, respectively. The $\sigma_a^2$and σ_e^2were the additive and residual variances, respectively. Residual variance (σ_e^2) was constrained to be equal to 1 in accordance with the specifications of a maximum a posteriori (MAP) probit threshold model (Gianola and Foulley, 1993).

In addition, a univariate linear BLUP animal model (LM) was used to evaluate HP on the observed scale. Though typically heritability estimates for binary cow fertility traits are higher when using a TM or when phenotypes are adjusted to a normal basis (Milagres et al., 1979; Van Vleck, 1971), the challenges with ECP and lack of support in the Super-Hybrid marker effects model (SMEM) justified the investigation of a LM for the prediction of HP. The model equation for the LM in matrix form is presented in equation 4.4:

$$y = Xb + Zu + e \quad \text{Eq. 4.4}$$

where $\boldsymbol{y}$ was a vector of binary HP observations, $\mathbf{X}$ was an incidence matrix relating observations in $\boldsymbol{y}$ to fixed effects, $\boldsymbol{b}$ was a vector of unknown solutions for fixed effects including CG, breed proportion, RHV, and YAGE, Z was an incidence matrix relating observations in $\boldsymbol{y}$ to random animal effects, u was a vector of random animal effects for AFC, and $\boldsymbol{e}$ was a vector of random residuals. It was assumed that residual effects, including random environmental and non-additive genetic effects are independently distributed with variance σ_e^2, so that $var(e) = I\sigma_e^2 = R; var(u) = A\sigma_a^2 = G$, and $cov(u, e) = cov(e, u) = 0$, where A is the numerator relationship matrix. For both model types, heritability estimates were obtained by calculating the ratio of the additive variance over the phenotypic variance.

4.2.4 Statistical analysis

Data preparation was performed with the Animal Breeder's Tool Kit (ABTK; Golden et al., 1995) package of tools on the Colorado State University Center for Genetic Evaluation of Livestock (CGEL). Variance parameter estimates, breeding values, and fixed effect solutions were obtained with restricted estimate maximum likelihood (REML) analysis using ASReml3.0 (Gilmour et al., 2009). Table 4.2 provides the description of all LM and TM performed across the various breed populations. Independent breed populations were run separately (Models 1-23) with relevant fixed effects, and records were then combined into a singular multi-breed population (Models 24-27).

Table 4.2. Description of linear models (LM) and threshold models (TM) used to generate variance components, genetic parameter estimates, random effect solutions, and fixed effect solutions for heifer pregnancy (HP) in various breed populations.

Model Number						
LM	TM	**Population**[¥]	**Fixed Effects**	**n of HP Records**	**n of Sires**	**n of Dams**
1	15	All SIMUSA	CG, YAGE*	52,967	12,242	72,481
2	16	SIMUSA >7/8 SIM	CG, YAGE**	4,534	3,070	9,688
3	17	All SIMUSA	CG, ∝SIM, ∝AAN, RHV, YAGE**	151,595	24,420	164,242
4	18	All RANUSA	CG, ∝AAN, ∝RAN, YAGE*	64,545	13,626	75,275
5	19	RANUSA >7/8 RAN	CG, YAGE*	18,156	5,325	27,815
6	20	All GBVUSA	CG, RHV, YAGE*	54,133	13,693	81,330
7	21	All LIMUSA	CG, YAGE*	71,117	14,748	106,389
8	22	All LIMUSA	CG, ∝LIM, RHV, YAGE*	71,117	14,748	106,389
9	23	All LIMCAN	CG, YAGE*	4,010	3,594	10,522
10	24	All LIMCAN	CG, ∝LIM, RHV, YAGE*	4,010	3,594	10,522
11	25	All BSHUSA	CG, YAGE*	899	1,352	3,134
12	26	All BSHUSA	CG, ∝BSH, RHV, YAGE*	899	1,352	3,134
13	27	Multi-breed	CG, YAGE*	178,672	41,004	250,811
14	28	Multi-breed	CG, [£] Breed ∝, RHV, YAGE*	178,672	41,004	250,811

¥ Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022).
£ Where all breed proportions (SIM, AAN, GBV, LIM, RAN, DAIRY, ENGL, CONT, UNK) were included and when added summed to 1.
* Limited records to only heifers that had a reported yearling age (YAGE) observation.
** Allowed heifers without a YAGE observation to be included in the evaluation. YAGE were treated as missing values for each heifer.
*** $\propto$ = Proportion

In some populations, there were fewer animals with records for both HP and YAGE. To boost the statistical power of the evaluation, some models were performed with animals that had an HP phenotype but had a missing YAGE phenotype. These models are indicated in Table 4.2. The number of sires and number of dams were the count of unique animals in the 3-generation pedigree obtained for each population. Summary statistics for the fixed effects used in the combined multi-breed population, fitting

all breed effects, and estimates of RHV (Models 14 and 28) are presented in Table 4.3. Appendix Table A-1 lists all International Committee for Animal Recording (ICAR) breed codes used to designate breed populations.

Table 4.3. Summary statistics for all fixed effects used in linear and threshold models for the evaluation of heifer pregnancy (HP) in a multi-breed population of heifers (n=178,672).

Term	n=0 ψ	Min	Mean	Max	SD
HP **	30,592	0	0.83	1.0	0.378
YAGE (d)	0	270	371.5	500	35.85
RHV (∝)	2,486	0	0.395	1.0	0.229
∝ SIM	125,423	0	0.157	1.0	0.278
∝ AAN	20,811	0	0.196	1.0	0.204
∝ GBV	151,539	0	0.063	0.919	0.166
∝ LIM	136,588	0	0.193	1.0	0.362
∝ RAN	46,026	0	0.306	1.0	0.387
∝ DAIRY	114,016	0	0.002	0.57	0.016
∝ ENGL	85,461	0	0.019	1.0	0.052
∝ CONT	117,045	0	0.004	0.996	0.019
∝ UNK	79,453	0	0.059	1.0	0.136

ψ where n=0 represents the number of animals with a 0 observation for each fixed effect. In the case of the breed proportions, this would indicate an animal has no ancestry to a particular breed.
¥ Breed proportions: SIM = Simmental, AAN = Black Angus, GBV = Gelbvieh, LIM = Limousin, RAN = Red Angus, DAIRY = All dairy breeds, ENGL = Other English breeds, CONT = Other Continental breeds, and UNK = Other or Unknown.
* Heifer pregnancy (HP) observations (1 = Success; 0 = Failure)
** Retained hybrid vigor (RHV)
*** ∝ = Proportion

4.2.5 Genetic evaluation validation

Models for genetic evaluation are inherently imprecise, especially with lowly heritable traits, and a primary objective of this study was choosing the most appropriate model for the evaluation of HP. Evaluating genetic models for evidence of bias, dispersion, and poor prediction accuracy can help validate and compare genetic evaluation methods. Methods described by Legarra and Reverter (2018) provide a framework for evaluating the correctness of models used for genetic evaluation. The procedures used involve estimating breeding values on a "whole" population and a "partial" population. The partial

population is established by identifying a "focal" group of animals in a population and censoring their records. The focal population is typically derived from younger generations so that family relationships and historical observations can predict the future performance of progeny. The estimated breeding value (EBV) obtained from an evaluation of the whole population is assumed to be closer to a true breeding value because all records are utilized and thus more accurate, and the EBV obtained on focal animals with censored records is based solely on historical records from family relationships. In general, genetic evaluations do not need to be based on mixed models, but the validation procedures presented by Legarra and Reverter (2018) are most commonly applied to mixed models and can be an excellent approach to validation of genetic evaluations. The precision of the estimators of accuracy, bias, and dispersion, however, depends on the distributional properties of the EBV and true breeding values (TBV).

A subset of the procedures described by Legarra and Reverter (2018) were used in the present study to compare bias, dispersion, and prediction accuracy for the evaluation of HP across LM and TM in different populations. Let $\boldsymbol{u}$ be the TBV and $\hat{u}$ an estimated EBV of a single individual, and the classical definition of accuracy is the correlation between the true breeding value and the estimated breeding value for an individual across repeated sampling. This can be shown theoretically in Equation 4.5:

$$r(u,\hat{u}) = \frac{cov(u,\hat{u})}{\sqrt{var(\hat{u})var(u)}} \quad \text{Eq. 4.5}$$

where the covariance between the estimated and true breeding values is the numerator, and the square root of the product of the estimated and true breeding value variances is the denominator. However, the true breeding value is never known in an animal. So, for the joint evaluation of all animals, the relevant measure of accuracy (Bijma et al., 2012) is the correlation between the TBV and EBV among the candidates for selection, which is a property of a population rather than an individual. This "population accuracy" is described in Equation 4.5 across a series of individuals in a population which is equivalent to classical accuracy (BIF, 2024) in cross-validation procedures, as shown by Legarra and Reverter (2018). Classical accuracy ($r_{EBV,BV}$) is defined in Equation 4.6.

$$r_{EBV,BV} = \sqrt{1 - \frac{Prediction\ Error\ Variance\ (PEV)}{Additive\ Genetic\ Variance\ (\sigma_a^2)}} \quad \text{Eq. 4.6}$$

such that $r_{EBV,BV}$ on animals from the whole population (acc_w) and on animals from the partial population (acc_p) are obtained. Of course, the additive genetic variance in the denominator term should be multiplied by one plus the inbreeding coefficient (F) for each animal. Bias is then defined as the difference between $\hat{u} - u$, and dispersion is defined as the slope of the regression of u on $\hat{u}$: $cov(u, \hat{u})/var(\hat{u})$. The procedures used to cross-validate LM and TM models used in this study were 1) the comparison of means of EBV from whole and EBV from partial data (Eq. 4.7), 2) the regression of EBV from whole data on EBV from partial data (Eq. 4.8), 3) the correlation of EBV from whole data and EBV from partial data (Eq. 4.9), and 4) the regression of EBV from partial data on EBV from whole data (Eq. 4.10). An explanation for Equation 4.7 is as follows:

$$\hat{\Delta}_p = \bar{\hat{u}}_p - \bar{\hat{u}}_w \quad \text{Eq. 4.7}$$

where $\hat{u}_p$ were the EBV from the partial population, and $\hat{u}_w$ were the EBV from the whole population, where the difference in the mean EBV from partial ($\bar{\hat{u}}_p$) and the mean EBV from the whole ($\bar{\hat{u}}_w$) datasets indicate evidence of bias in the evaluation. An ideal value is 0 if the evaluation is unbiased. Values that were >0 represented overestimation of the genetic differences, whereas values <0 represented underestimation of genetic differences. Using linear regression statistical methods, we can also obtain evidence of dispersion using Equation 4.8:

$$b_{w,p} = \frac{cov(\hat{u}_p, \hat{u}_w)}{var(\hat{u}_p)} \quad \text{Eq. 4.8}$$

where $b_{w,p}$ represented the slope of the EBV values obtained from the whole and partial evaluations. The expected value of the slope is 1, suggesting that the closer a value is to 1, the less dispersed the evaluation method was. Values less than 1 indicated over dispersion, and values greater than 1 indicated under dispersion of EBV. The next procedure is the correlation of EBV from whole and the EBV from partial data, described in Equation 4.9.

$$\rho_{w,p} = \frac{cov(\hat{u}_p, \hat{u}_w)}{\sqrt{var(\hat{u}_w) var(\hat{u}_p)}} \quad \text{Eq. 4.9}$$

where $\rho_{w,p}$ was the correlation between the EBV estimated from the whole and partial datasets. The expected value for this correlation is the increase in population accuracy of EBV from partial and whole datasets, which is equivalent to $\frac{acc_p}{acc_w}$, though an ideal value would be near 1 (but not exactly 1). Returning a value of 1 would suggest that an additional 10 years of data would not change predictions, which is impossible. However, a higher correlation suggests that EBV from the partial dataset are a reliable source of information for the future prediction of phenotypes. The higher the value (>1) the lower the correlation between the partial and whole datasets. The regression of EBV from partial data on the EBV from whole data follows a similar structure and is described in Equation 4.10.

$$b_{p,w} = \frac{cov(\hat{u}_p, \hat{u}_w)}{var(\hat{u}_w)} \quad \text{Eq. 4.10}$$

where $b_{p,w}$ was the slope of the regression of the EBV from partial data on the EBV from the whole dataset. The expected value of this regression is the squared increase in population accuracy (reliability) of EBV from partial and whole datasets, which is equivalent to $\frac{{acc_p}^2}{{acc_w}^2}$. The estimate for $b_{p,w}$ is then a ratio of dispersions, and the difference in the expected value and the observed value is the magnitude of dispersion in the evaluation.

The statistical procedures described above were tested on competing LM and TM models using data from independent Red Angus, Simmental, and multi-breed populations. A full and partial run were performed for each evaluation and then summary statistics were calculated. The partial dataset censored the most recent 5 years of HP phenotypes, and animals with their phenotypes censored were called the "validation" group. In the Red Angus population, this resulted in 10,175 validation animals (~16% of entire population). In the Simmental population, this resulted in 11,850 validation animals (~47% of the entire population). The Simmental population used for validation was based on Model 26, where all SIMUSA animals with >50% Simmental breed proportion were included. The multi-breed population was the same as those used in models 24-27 and 51-54. In all three populations, all animals without a YAGE observation were excluded. After censoring the most recent 5 years of HP phenotypes, this resulted in a

validation group of 46,151 heifers (~26% of the entire population). Pearson correlations between the EBV obtained from the partial population and EBV obtained from the whole population were estimated. In addition, average Beef Improvement Federation accuracy (BIFacc) values on the EBV from LM and TM were obtained on the validation group of heifers in each population. The equation used to obtain BIFacc is described in Equation 4.11. Traditional accuracy ($r_{ebv,bv}$) can be obtained from BIFacc with the method described in Equation 4.12. Variance components were estimated and EBV were obtained from the solutions file (.sln).

$$BIF_{acc} = 1 - \sqrt{\frac{PEV}{Additive\ Variance\ (1+F)}} \quad \text{Eq. 4.11}$$

where the prediction error variance (PEV) was obtained from the standard error of prediction (SEP) estimated for all animals and converting SEP to PEV is described below:

$$BIF_{acc} = 1 - \sqrt{\frac{SEP^2}{Additive\ Variance\ (1+F)}}$$

which can then be used to obtain the traditional definition of $r_{ebv,bv}$ as described by BIF (2024):

$$r_{ebv,bv} = \sqrt{1 - (1 - BIF_{acc})^2} \quad \text{Eq. 4.12}$$

4.3 Results and Discussion

In general, reproductive rates of first breeding in beef heifers range from 64% to 95%, according to Moorey and Biase (2020). On average, 85% of beef heifers become pregnant by the completion of the breeding season, and no meaningful trends for decreasing or increasing pregnancy rates have generally been observed. The dataset in this study combines historical observations across numerous breed populations and, for this reason, can provide a glimpse into potential phenotypic trends for heifer fertility. Figure 4.1 provides the average pregnancy rates in a combined multi-breed population since 1980. We observed that there has been a modest decrease in the average pregnancy percentages in heifers since 1980. The average annual decrease has been minimal at -0.27% per year since 1980 (R^2 = 0.66), but still suggests a modest and consistent decline in heifer pregnancy rates. This can be concerning, as beef

producers often provide ample opportunity for heifers to become pregnant with extended breeding seasons and with the use of artificial insemination.

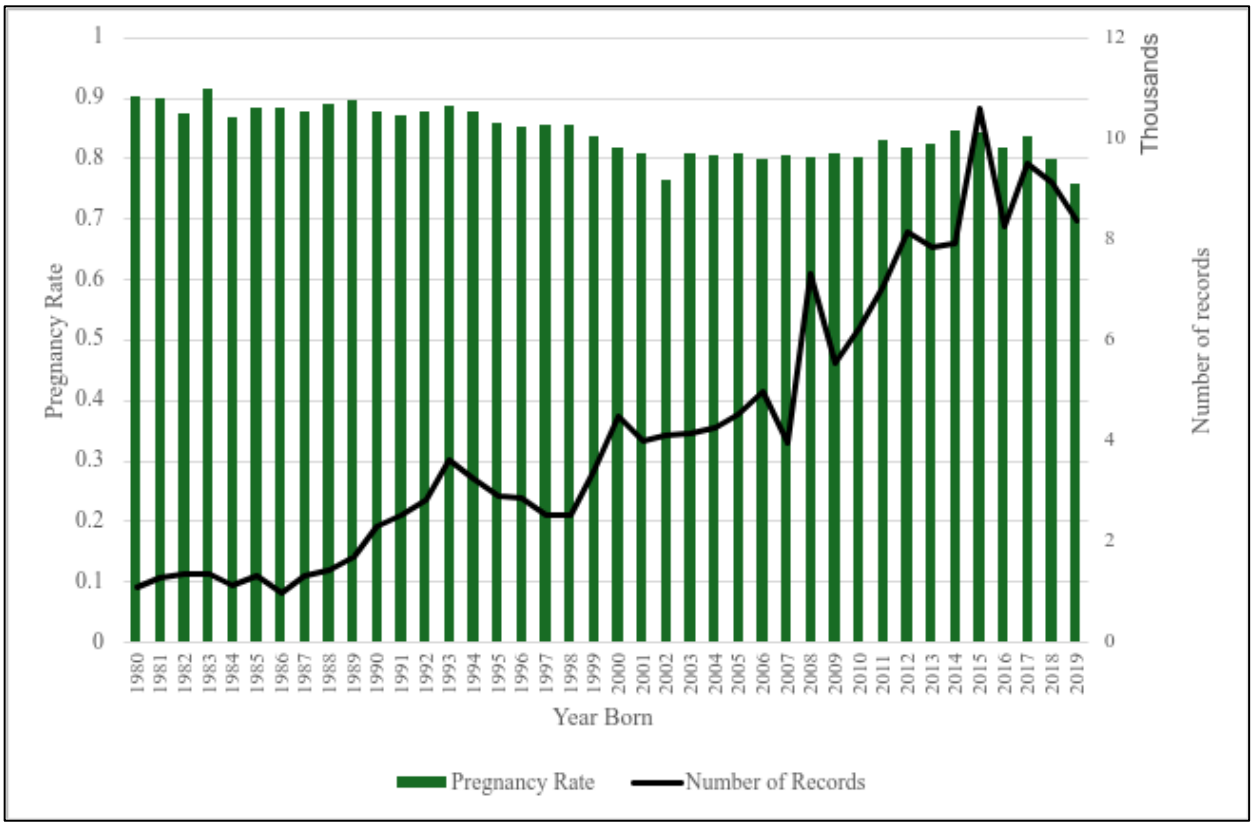

Figure 4.1. Pregnancy rate by year of birth in a multi-breed population (n=178,762) of beef heifers since 1980.

A possible explanation for this decreasing trend is that HP data were sparsely reported up until the early 2000s and whole herd reporting programs (WHR) were not generally implemented until the late 1990s. For this reason, heifers that failed to breed were likely removed from the herd and not reported to their respective breed organization. The average annual change in pregnancy rate from 2000 to 2019 is +0.07% (R^2 = 0.04), suggesting this may be a likely explanation. The multi-breed population presented in Figure 4.1 is agnostic of breed and does not account for possible breed differences. Figure 4.2 provides the historical average annual change in pregnancy rate from 1980 to 2019 using raw data reported to IGS separated out by 4 breed populations (GBVUSA, LIMUSA, RANUSA, and SIMUSA). There were no RANUSA HP records reported until 1988, and no SIMUSA HP records reported until 2006.

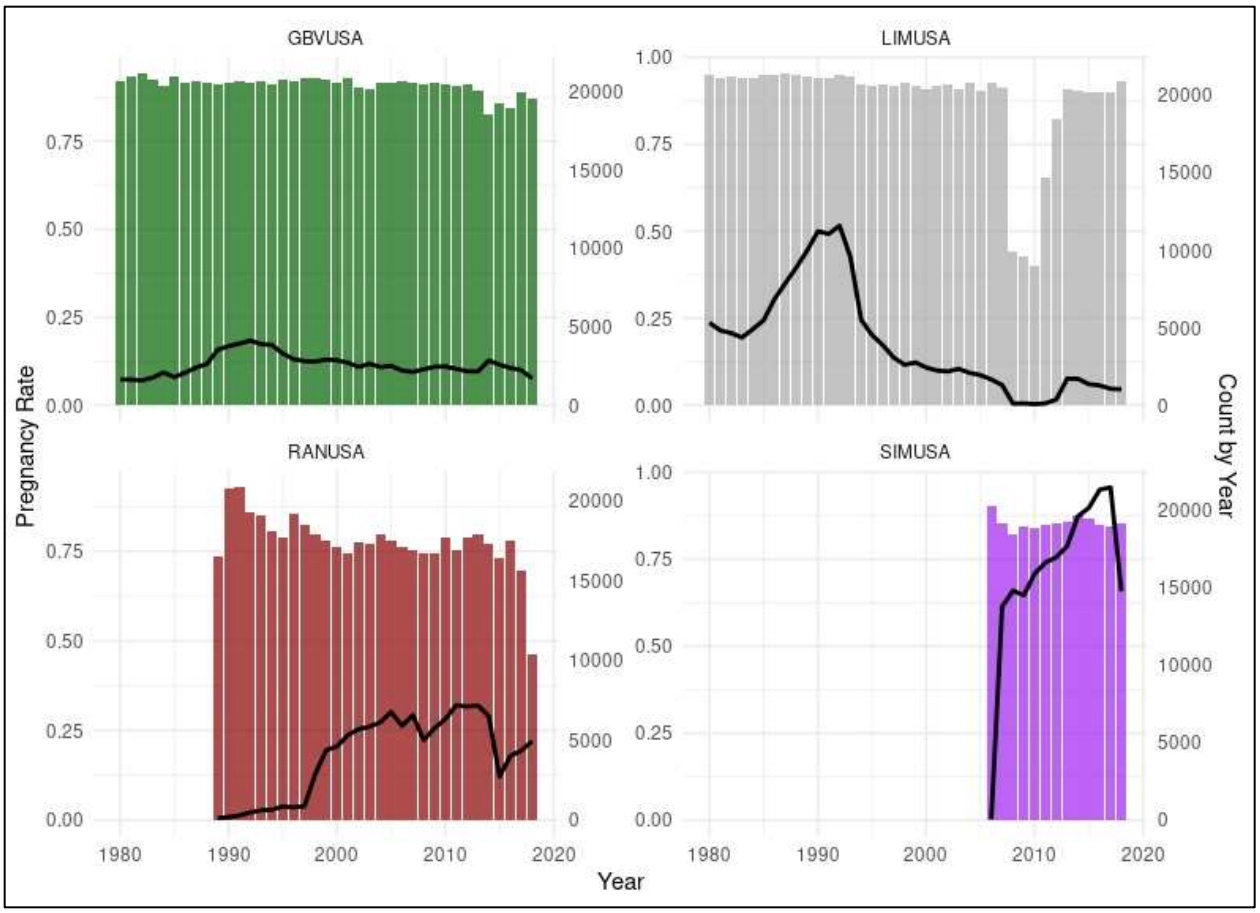

Figure 4.2. Pregnancy rate by year of birth since 1980 and the relationship with data reporting in Gelbvieh (GBVUSA), Limousin (LIMUSA), Red Angus (RANUSA), and Simmental heifers (SIMUSA).

The data from Figure 4.2 show differences in the pregnancy rate historical trends. Particularly, Red Angus appear to have a meaningful decrease in pregnancy rates annually at -0.56% (R^2=0.39), though 2018 appears to be an outlier in these data. This is especially concerning, as the RAAA has had a genetic prediction for improved HP since the early 2000's, and no major decrease in genetic trend for HP has been observed. The other three breeds (GBVUSA, LIMUSA, and SIMUSA) all appear to have a relatively flat trendline for HP over time, except for a major decrease in HP data reporting and average pregnancy rate in LIMUSA from 2008-2011. It's not immediately clear for the reason of this decrease in data reporting and average pregnancy rate in Limousin heifers. The GBVUSA population had a decreasing HP phenotypic trend of -0.14% (R^2=0.43), the LIMUSA population had a decreasing HP

phenotypic trend of -0.51% (R^2=0.17), and the SIMUSA population had a decreasing HP phenotypic trend of -0.04% (R^2=0.01). It's clear that the large inclusion of SIMUSA data from 2006 to the present makes up a majority of the data reporting increase observed in the same time frame from Figure 4.1. Since the records from SIMUSA are derived from converting WHR data into HP observations, perhaps the different trait definition is introducing bias into the historical pregnancy rate trends observed in other breed populations as seen in Figure 4.1. However, removal of all SIMUSA data did not change the observed decrease in average pregnancy rates across breed populations with a decreasing pregnancy rate trendline of -0.38% (R^2=0.72). For these reasons, there is evidence that a decreasing trend in average pregnancy rates across breed populations is being observed. Figure 4.3 provides the average pregnancy rate across all years separated by breed population.

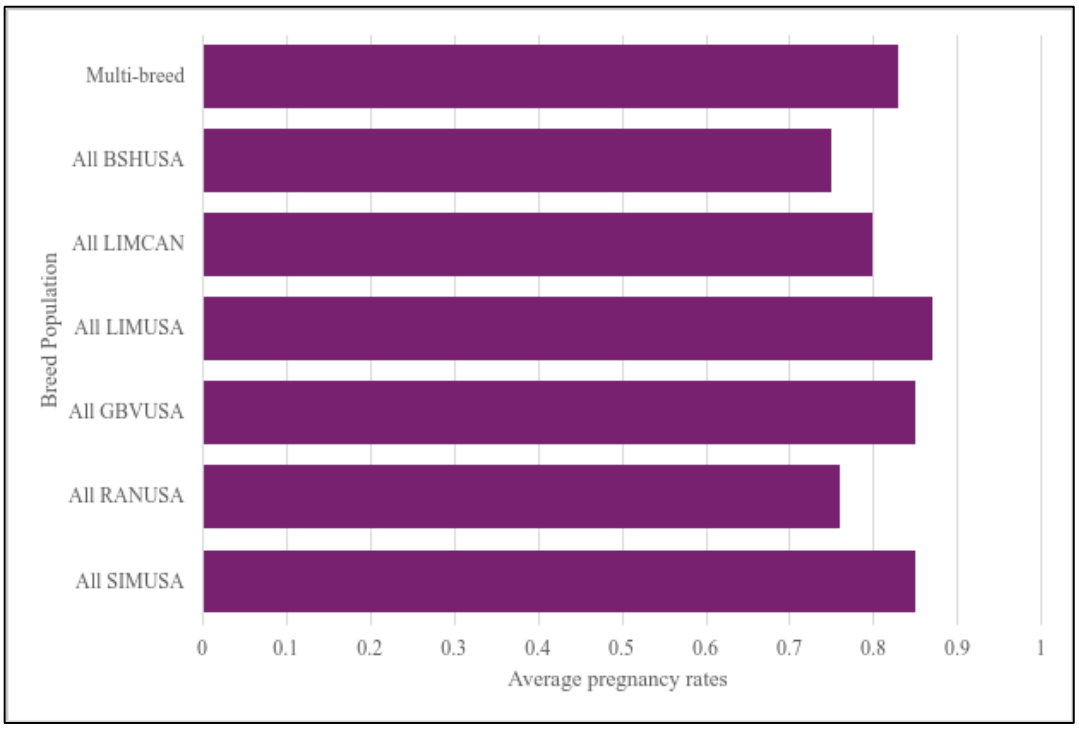

Figure 4.3. Average pregnancy rates in first calf heifers by breed population.

* Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022).
** Heifer pregnancy (HP) observations (1 = Success; 0 = Failure) were reported to IGS, though each breed association may have their own nuanced definition of HP.

4.3.1 Genetic parameter estimates for heifer pregnancy using linear and threshold models

The average pregnancy rate in the multi-breed population was 83%, and across all years, Shorthorn (BSH) and Red Angus (RAN) heifers had the poorest pregnancy rates, and Limousin USA (LIM) and Simmental (SIM) heifers had the highest pregnancy rates. While it is unclear why BSH and RAN heifers had poorer reported pregnancy rates compared to other breed populations, this could be due to more restrictive data reporting. For example, heifer pregnancy data reported to the Red Angus Association is member-submitted and typically requires elaborate reporting of breeding season length, AI dates, and is considered by some as the "gold standard" of fertility data reported to any beef breed association. Perhaps more stringent reporting requirements are improving the integrity of the data being reported. The average pregnancy rate for Red Angus was 0.76, which was consistent with the mean presented by Boldt et al. (2018). However, there is still ample variation in all populations necessary for genetic evaluation. Variance components for the LM methods used in models 1-12 are presented in Table 4.4.

Table 4.4. Genetic parameter estimates for heifer pregnancy (HP) using linear models (LM) in Simmental, Red Angus, Gelbvieh, Limousin, and Shorthorn populations.

Model¥	n	σ_a^2	σ_e^2	σ_p^2	h^2	*se*
1	52,967	0.003	0.116	0.119	0.029	0.006
2	4,534	0.004	0.175	0.179	0.024	0.030
3	151,595	0.011	0.121	0.133	0.084	0.005
4	64,545	0.008	0.148	0.156	0.051	0.007
5	18,156	0.004	0.161	0.164	0.022	0.010
6	54,133	0.001	0.119	0.120	0.008	0.004
7	71,117	0.001	0.108	0.109	0.006	0.003
8	71,117	0.001	0.108	0.109	0.006	0.003
9	4,010	0.006	0.147	0.153	0.040	0.034
10	4,010	0.006	0.147	0.153	0.040	0.035
11	899	0.67E-7	0.181	0.181	0.000	NE*
12	899	0.23E-7	0.180	0.180	0.000	NE *

¥ Where models 1-3 involved Simmental USA (SIMUSA) populations, models 4 &5 involved Red Angus USA (RANUSA) populations, model 6 involved Gelbvieh USA (GBVUSA) animals, models 7-10 involved Limousin USA (LIMUSA) and Limousin Canada (LIMCAN) populations, and models 11 & 12 involved Shorthorn USA (BSHUSA) populations.
* NE = Not estimable

The average heritability estimate for HP across breed populations using LM methods (Table 4.4) was 0.026, with a minimum value of 0 and a maximum of 0.084. Heritability estimates for HP on the observed scale using LM methods are generally low (Dearborn et al., 1973; Milagres et al., 1979; Toelle and Robinson, 1985). Weik et al. (2021) performed a similar comparison study of LM and TM for the evaluation of HP in a multi-breed population of New Zealand heifers and reported a heritability of 0 using an LM. Buddenberg et al. (1989) reported HP heritability estimates on the observed scale of 0.17, 0.04, and 0.05 for Angus, Hereford, and Polled Hereford, respectively. Though their observed heritability estimate for Angus was considerably higher than many of the estimates in these populations, those in the Hereford populations are consistent with HP heritability estimates in the present study. Across all populations, heritability estimates were low to near zero except in Model 3, which used an all SIMUSA population and allowed for missing YAGE observations. Though this population was considerably larger

than other breed populations evaluated in the study, the residual and phenotypic variances were similar, suggesting that the results are reliable. In the Simmental population that was censored to only include animals with Simmental breed proportion >7/8, however, the heritability estimate was much lower. A possible explanation for this is that the ASA breed registry identifies two separate populations of high percentage Simmental, with “Fullblood” status being awarded to Simmental animals that are 100% Simmental and can be traced back to Fleckvieh ancestry in Europe and “Purebred” status being awarded to Simmental animals that are 7/8 or greater Simmental and out of registered Simmental parents. This could allude to the fact that Fullblood and Purebred Simmental populations may have considerably diverged in breed type. The heritability estimates from the Red Angus populations were higher than those in the Gelbvieh, Limousin, and Shorthorn populations. This is worth noting that the RAAA has more robust HP data recording than all other breed associations represented in this study.

Doyle et al. (2000) concluded that evaluating HP on the observed scale generally leads to lower heritability than when evaluating HP on the underlying scale, and thus, the use of TM may be a more appropriate evaluation strategy. Table 4.5 provides the genetic parameter estimates for HP on the underlying scale using TM evaluation methods.

Table 4.5. Genetic parameter estimates for heifer pregnancy (HP) using threshold models (TM) in Simmental, Red Angus, Gelbvieh, Limousin, and Shorthorn populations.

Model¥	n	σ_a^2	σ_e^2	σ_p^2	h^2	*se*
15	52,967	0.071	1.0	1.071	0.066	0.011
16	4,534	0.273	1.0	1.273	0.214	0.034
17	151,595	0.118	1.0	1.118	0.106	0.006
18	64,545	0.101	1.0	1.101	0.092	0.009
19	18,156	0.136	1.0	1.136	0.120	0.018
20	54,133	0.143	1.0	1.143	0.125	0.013
21	71,117	0.159	1.0	1.159	0.137	0.012
22	71,117	0.159	1.0	1.159	0.137	0.012
23	4,010	0.280	1.0	1.280	0.219	0.038
24	4,010	0.282	1.0	1.282	0.220	0.038
25	899	0.381	1.0	1.381	0.276	0.073
26	899	0.388	1.0	1.388	0.279	0.073

¥ Where models 15-17 involved Simmental USA (SIMUSA) populations, models 18 & 19 involved Red Angus USA (RANUSA) populations, model 20 involved Gelbvieh USA (GBVUSA) heifers, models 21-24 involved Limousin USA (LIMUSA) and Limousin Canada (LIMCAN) populations, and models 25 & 26 involved Shorthorn USA (BSHUSA) populations.

The average heritability for HP using TM methods (Table 4.5) was 0.17, with a minimum of 0.07 and a maximum of 0.28. Of the populations represented in this study, Shorthorn had the highest heritability using TM; however, due to fewer animals with observations, they also had the highest standard error. Simmental heifers had the lowest heritability out of all the breeds represented. However, this could be due to the difference in how HP phenotypes are assigned using WHR codes, as described in Chapter 3. However, all estimates in Table 4.5 are consistent with those reported in the literature (Cammack et al., 2009). Doyle et al. (2000) reported an average heritability estimate on the underlying scale of 0.21 in Angus heifers. In a more recent population of Red Angus heifers, with data being provided by the Red Angus Association of America (RAAA), McAllister et al. (2011) reported a heritability estimate of 0.17 on the underlying scale. Boldt et al. (2018) continued the investigation into fertility traits of RAAA animals and, with a decade of additional records, reported an average heritability estimate of 0.12 for HP using TM methodology. Despite records being obtained from the same source at

the RAAA, the heritability estimates for Red Angus populations in the present study were lower than those reported by Boldt et al. (2018). This could be due to differences in how CG were defined in the present study compared to how Boldt et al. (2018) defined CG. The RAAA enforces a threshold on pregnancy success within a 90-d breeding seasons, such that even heifers that become pregnant outside of 90-d will still receive a failure observation. Because breeding season length is largely unknown among data reported to IGS, there was no discrimination in pregnancy success outside of a 90-d threshold in the present study. Comstock (2009) explained that heritability estimates for HP generally decreased as breeding season length increased. This indicates that extra time and opportunity to become pregnant could eliminate some of the additive variance for overall fertility expressed in the population. Boldt et al. (2018) reported an additive variance of 0.14, whereas in the present study's defined population of Red Angus, there was a 0.10 additive variance estimate. Due to data reporting across the various breed associations, defining breeding season length is unattainable without making assumptions on gestation length and so was not initially included in the present study's CG definition.

These literature results support the present study's findings that HP is a lowly heritable trait across a variety of breed populations. An important distinction is that across all models in Table 4.5, when RHV ($P<0.001$) or breed proportions were included as factors, there was minimal change in variance estimates. In all models, CG and YAGE were significant fixed effects ($P<0.001$). Most of the change in variances in the Simmental populations (Models 15-17) are likely attributed to changes in population size and classification. These results and those reported by Buddenberg et al. (1989) suggest notable breed differences are influencing HP phenotypes and can be a considerable factor when considering developing a multi-breed HP genetic evaluation. To best estimate variance components and fixed effect solutions for breed proportion and RHV, a multi-breed population combining all HP observations was established. Table 4.6 provides the variance components for a series of LM and TM in a combined multi-breed population (n=178,672).

Table 4.6. Genetic parameter estimates for heifer pregnancy (HP) using a series of competing linear models (LM) and threshold models (TM) fitting different fixed effects in a multi-breed population (n=178,672) of heifers.

Model	Fixed Effects	σ_a^2	σ_e^2	σ_p^2	h^2	*se*
Linear Models						
13	CG, YAGE	0.003	0.125	0.128	0.023	0.003
14	CG, £ Breed ∝, RHV, YAGE	0.003	0.125	0.128	0.024	0.003
Threshold Models						
27	CG, YAGE	0.096	1	1.096	0.088	0.006
28	CG, £ Breed ∝, RHV, YAGE	0.096	1	1.096	0.088	0.006

£ Where all breed proportions (SIM, AAN, GBV, LIM, RAN, DAIRY, ENGL, CONT, UNK) were included and when added summed to 1.
* CG = Contemporary Group; YAGE = Yearling Age (d); RHV = Retained Hybrid Vigor (∝)
** ∝ = Proportion

The estimates of additive variance, residual variance, and heritability were essentially the same in the LM model, fitting only CG and YAGE (Model 13) compared to the full fit model (Model 14) which included breed proportion and RHV. This trend was consistent in the TM models (Models 27 & 28). The large size and broad scale of the multi-breed population may dilute the ability of the evaluations to effectively isolate genetic variability for breed differences and heterosis factors. It could be reasoned that with so many animals evaluated, the sensitivity of the evaluation is being negatively impacted. However, when comparing variance estimates from the multi-breed evaluation models to those from the independent breed population models, variance components were uniform. The LM indicates HP is a lowly heritable trait on the observed scale, but if heritability estimates were converted to the underlying scale they may be equivalent with heritability estimates obtained from TM. Compared to the independent breed populations, the additive genetic variance was lower when all breeds were combined. Some of this could be explained by the addition of breed effects and heterosis, and so Table 4.7 provides the Wald F statistics and solutions for fixed effects from models 14 and 28 as they were the most complete evaluations and fit all relevant effects.

Table 4.7. Wald F statistics and solutions for fixed effects for the evaluation of heifer pregnancy (HP) in a multi-breed population of heifers using linear model (LM) and threshold model (TM) methods.

	Linear Models			*Threshold Models*		
Effect £	F-Inc	Solution	*P-value*	F-Inc	Solution	*P-value*
YAGE	125.61	0.0005	<0.001	118.1	0.002	<0.001
∝ SIM	0.94	0.102	0.334	0.87	0.444	0.353
∝ AAN	2.34	0.079	0.129	1.76	0.337	0.187
∝ GBV	0.9	0.109	0.345	0.72	0.493	0.396
∝ LIM	0.16	0.119	0.682	0.18	0.544	0.67
∝ RAN	9.77	0.095	0.002	8.5	0.414	0.004
∝ DAIRY	0.58	0.071	0.447	0.35	0.272	0.549
∝ ENGL	5.51	0.069	0.02	4.61	0.307	0.033
∝ CONT	0.64	0.027	0.422	0.59	0.117	0.441
RHV	26.06	0.036	<0.001	27.69	0.172	<0.001

£ Where all breed proportions (SIM, AAN, GBV, LIM, RAN, DAIRY, ENGL, CONT, UNK) were included and when added summed to 1.
* Breed proportions: SIM = Simmental, AAN = Black Angus, GBV = Gelbvieh, LIM = Limousin, RAN = Red Angus, DAIRY = All dairy breeds, ENGL = Other English breeds, CONT = Other Continental breeds, and UNK = Other or Unknown.
** CG = Contemporary Group; YAGE = Yearling Age (d); RHV = Retained Hybrid Vigor (∝)
*** ∝ = Proportion

The results from Table 4.7 show that YAGE and RHV were significant factors affecting HP; however, breed differences were more variable. The variable UNK was constrained, and no solutions were obtained. The use of TM allows us to directly interpret the impact of effects on the probability of HP. The effect for YAGE was significant ($P<0.05$) and resulted in a 0.2% increase in HP for each day increase in YAGE. This result is logical in that older heifers will have a greater opportunity to reach puberty and will have expressed estrus by the time of first exposure. The effect for RHV was significant ($P<0.05$) and resulted in a 17.2% increase in HP in heifers when maximum heterosis was present compared to straightbred heifers. Cundiff et al. (1974) provided groundbreaking work on the impact of heterosis on fertility. They showed that crossbred heifers that were managed to calve at 2-years-of-age

had a 12% higher likelihood of staying pregnant ($P<0.05$) than their straightbred counterparts (Cundiff et al., 1974). Their result is consistent with the present study's effect of 17.2%. Of the breed effects, RAN and ENGL were significant ($P<0.05$), where a change from the mean UNK animal to 100% RAN results in a 41.4% improvement in HP, and a change from the mean UNK animal to 100% ENGL results in 30.7% increase in HP. These results can be confusing, however, because of the inability to know what breed type is represented in the unknown category, and thus meaningful comparisons of these effects are impossible. Few studies have investigated specific breed differences related to HP, though Cundiff et al. (1993) reported breed means for pregnancy rate in heifers, and though differences in age at puberty were noted, conception rate in yearling heifers did not differ consistently between breed groups reaching puberty at the oldest ages from those breed groups reaching puberty at the youngest ages, under the same management considerations. Weik et al. (2021) fit breed effects as a fixed effect in their models but did not report solutions. To fully leverage the benefits of heterosis, utilizing diverse breeds is key. Since there are no significant differences in heifer pregnancy rates between breed types, producers can focus on optimizing the genetic potential for heifer pregnancy without worrying about potential setbacks associated with breed differences.

4.3.2 Validation of linear and threshold model heifer pregnancy evaluations

The previous results support the claim that TM may be the most appropriate for genetic evaluation of HP; however, due to the ECP and inability of TM support on BOLT evaluation software (Golden et al., 2018), the question of using LM as a viable alternative is presented. In addition, Meijering and Gianola (1985) suggested that when heritability estimates are obtained using TM methods, they can be unstable when the frequencies of the binary response variable are extreme, such as when they surpass the 80:20 threshold. In many of the populations evaluated in this study, the average pregnancy rate was >80%. Thompson (2001) summarized that fitting genetic models to data is an important way of testing genetic theories and correctly predicting the breeding values of animals. This can be a challenge in multi-trait, across country evaluation, as summarized by Schaeffer (1994), because if the genetic trend is not

correctly estimated, it can influence predictions of breeding values, thus influencing genetic selection and progress. The ability to determine the correctness of a model can be accomplished with the cross-validation procedures described by Legarra and Reverter (2018). Estimates of the difference in mean EBV from whole and partial data (μ_{wp}), regression of EBV from partial data on EBV from whole data (b_{pw}), regression of EBV from whole data on EBV from partial data (b_{wp}), and the correlation of EBV from whole data on the EBV from partial data (ρ_{wp}) can be indicators of bias, dispersion, and prediction accuracy. Figure 4.4 presents the estimates for these 4 procedures comparing LM and TM in Red Angus.

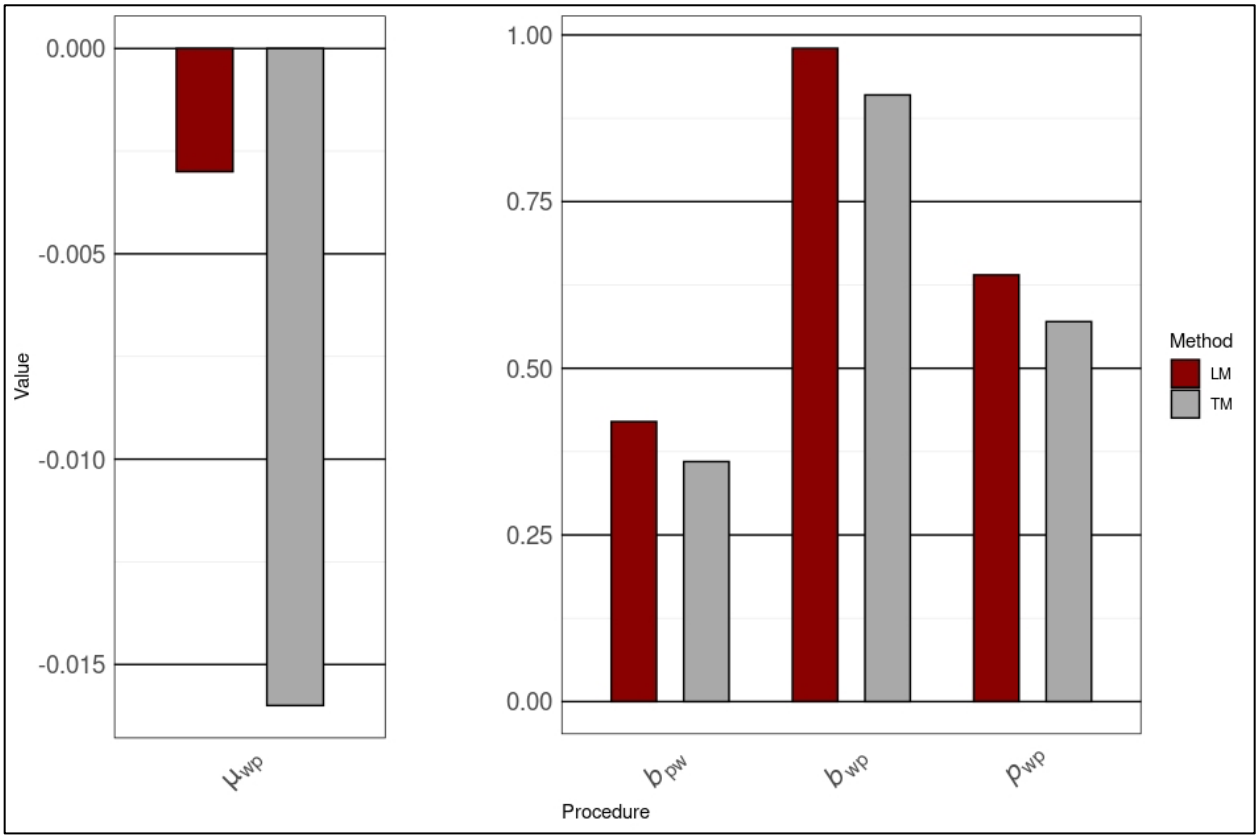

Figure 4.4. Estimates of validation statistics comparing linear models (LM) and threshold models (TM) for the prediction of heifer pregnancy (HP) in a population of Red Angus heifers.

* Where μ_{wp} = the difference in means of EBV estimated from whole data and EBV estimated from partial data evaluations, b_{pw} = the regression of EBV estimated from the partial data on the EBV from the whole data evaluations, b_{wp} = the regression of EBV estimated from whole data on EBV from the partial data evaluation, and ρ_{wp} = the correlation of EBV estimated from whole data on the EBV from partial data.

To start the validation of HP procedures, a data file from the RAAA was received to estimate validation statistics using their data structure, as opposed to the data received from IGS, which lacks the breeding season length knowledge. This was done to compare validation statistics using results from their evaluation to the results estimated from across breeds using the data received from IGS. There were 63,933 HP records, with a mean HP of 0.744. There were 22,157 unique sires and 104,346 unique dams in the 3-generation pedigree. Fixed effects were CG and AFE, which had minimum, mean, and maximum values of 300, 429.2, and 520, respectively. Variance components for HP were estimated directly from the whole dataset LM and TM evaluations. The heritability estimates for this population of Red Angus heifers using an LM were 0.05 ± 0.007 and 0.15 ± 0.009 using a TM. These results are consistent with heritability estimates obtained in evaluations of Red Angus from IGS data.

The "validation" group of heifers were the animals from the past 5 years, with their HP phenotypes censored in the partial evaluation. Comparing EBV and accuracy estimates in the whole population can misrepresent the magnitude of the cross-validation statistics as the values will be centered towards the mean of the ancestors. For this reason, the validation group of animals is compared across procedures. Because BIFacc is typically used in national cattle evaluation (NCE) to facilitate an understanding of prediction accuracy, one of the first validation statistics performed was to compare the average BIFacc of EBV estimated on validation heifers from whole and partial evaluations. The average BIF accuracy on Red Angus validation heifers was 0.07 and 0.03 for whole and partial LM evaluations, respectively, and 0.09 and 0.04 for whole and partial TM evaluations, respectively. This suggests the TM resulted in higher prediction accuracy than the LM, but this is expected because accuracy is a function of a trait's heritability, and the TM method for evaluation of HP generally resulted in higher heritability. Figure 4.4 shows the results of the cross-validation procedures. The first procedure is the difference in mean EBV with estimates of –0.003 and –0.016 for LM and TM respectively. The expected value for μ_{wp} is 0. This suggests that although both evaluation methods underestimate genetic differences, the values are essentially zero and show little evidence of bias in evaluation type. The estimates for b_{pw} were 0.42 and 0.36 for LM and TM, respectively. The expected value for this procedure is a function of the

respective population accuracies ($r_{EBV,BV}$) squared. The expected values for b_{pw} were 0.16 and 0.20 for LM and TM, respectively. The expected value of b_{pw} for TM was higher which means we would expect to see a higher proportional increase in the reliability of EBV from TM compared to the EBV from LM. The larger deviation of the estimate versus the expected value in the LM suggests there is a higher level of dispersion compared to the TM method. The values for b_{wp} were 0.98 and 0.91 for LM and TM methods, respectively. In comparison, the LM method was closer to 1 than the TM method, though both model approaches appeared to be performing well with little evidence of bias and dispersion. The estimates for ρ_{wp} were 0.64 and 0.57 using the LM and TM methods, respectively. An ideal estimate for ρ_{wp} is a value close to 1. Again, the LM and TM performed well and similarly with each other, suggesting reasonable prediction accuracy for both methods.

This procedure was replicated in a Simmental population consisting of only heifers with 50% or greater Simmental breed proportion. Since many animals of differing breeds are registered at the ASA, the population used for this validation procedure was designed to filter out as many breed differences as possible. The average HP pregnancy rate was 0.85. Fixed effects included RHV, SIM breed proportion, AAN breed proportion, other breeds proportion, and YAGE. The minimum, mean, and maximum RHV values were 0, 0.39, and 1, respectively. The minimum, mean, and maximum SIM proportions were 0.50, 0.75, and 1.0, respectively. The minimum, mean, and maximum AAN proportions were 0, 0.19, and 0.50 respectively. The minimum, mean, and maximum other breed proportions were 0, 0.06, and 0.50, respectively. The minimum, mean, and maximum YAGE were 270, 366, and 499, respectively. The heritability estimates on this population using an LM were 0.02 ± 0.007 and were 0.07 ± 0.016 using a TM.

Of the validation statistics performed in the Simmental population, the Pearson correlations between EBV from LM and EBV from TM in the whole population (LM_w on TM_w) and partial populations (LM_p on TM_p) were 0.98 and 0.98, respectively. This suggests the EBV produced from the LM were highly correlated with the EBV produced from the TM regardless of dataset used. However, the

Pearson correlations were 0.86 and 0.83 between the EBV from LM in the partial population with the EBV from LM in the whole population (LM_p on LM_w) and between the EBV from TM in the partial population with the EBV from the TM in the whole population (TM_p on TM_w). This shows that there is significant loss in statistical power and the EBV change when data are filtered out of the evaluation, as expected. The average BIFacc of the Simmental validation heifers in the partial dataset were 0.015 and 0.023 for LM and TM respectively, whereas the average BIFacc in the whole dataset was 0.038 and 0.057 for LM and TM respectively. Figure 4.5 displays the estimates for the cross-validation procedures in this Simmental population. The μ_{wp} estimates were 0.0003 and 0.001 for LM and TM, respectively, indicating there is marginally more evidence of bias in the TM method. Though with an ideal value of zero, both evaluation methods appear appropriate. The estimate for b_{wp} were 0.91 and 0.84 for LM and TM respectively, indicating again that both evaluation methods appear appropriate, though there is less evidence of bias and dispersion in the LM approach. The estimate for b_{pw} using LM was 0.457 with an expected value of 0.342, and for TM was 0.389 with an expected value of 0.392, indicating the TM method is more desirable due to the increase in accuracy and reliability of predictions. Finally, the ρ_{wp} in this Simmental population were 0.64 and 0.57 for LM and TM, respectively. With an ideal value of near 1, this indicates that both perform similarly and can be assumed appropriate for the prediction of HP. This group of Simmental heifers was filtered to eliminate any animals less than 50% $\propto$ SIM, and thus, CG structure may have been disrupted. However, despite the difference in breed type, these results are similar to those obtained from the Red Angus cross-validation procedures.

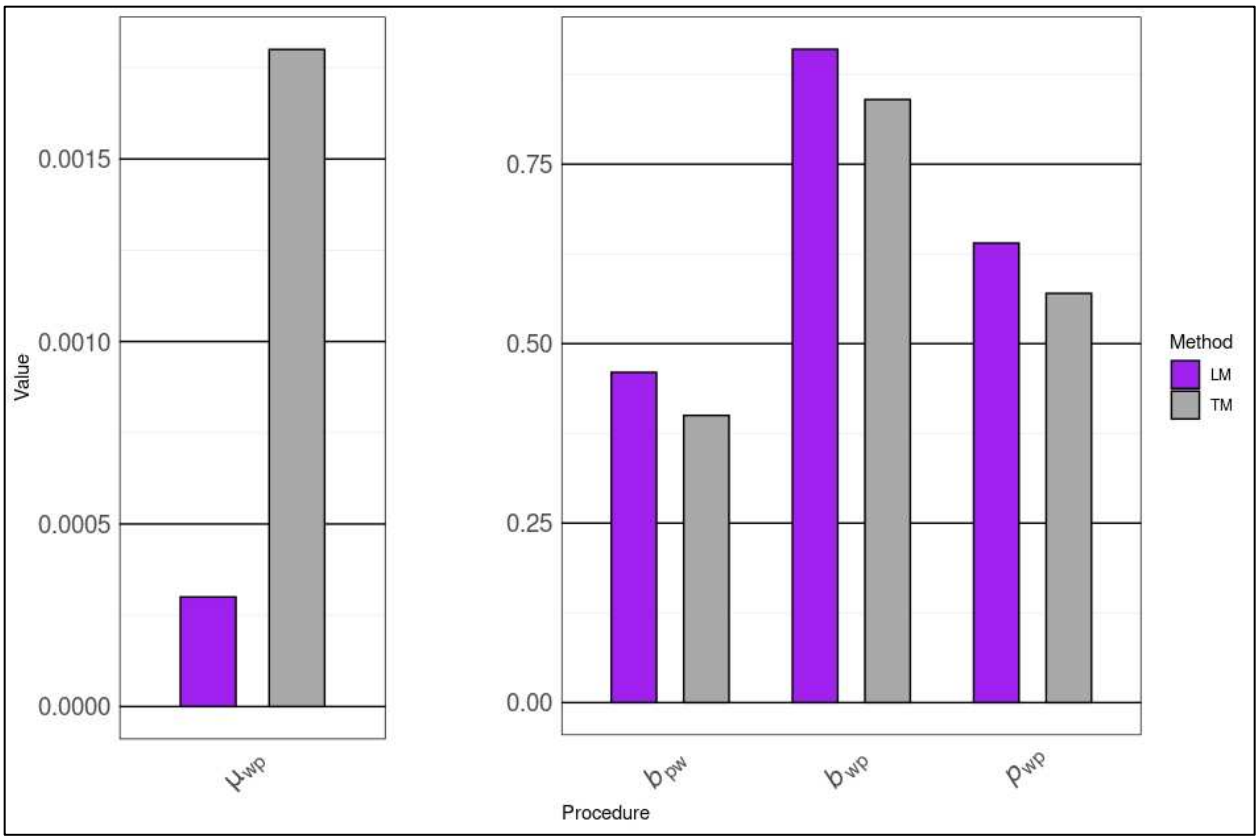

Figure 4.5. Estimates of validation statistics comparing linear models (LM) and threshold models (TM) for the prediction of heifer pregnancy (HP) in a population of Simmental heifers.

* Where μ_{wp} = the difference in means of EBV estimated from whole data and EBV estimated from partial data evaluations, b_{pw} = the regression of EBV estimated from the partial data on the EBV from the whole data evaluations, b_{wp} = the regression of EBV estimated from whole data on EBV from the partial data evaluation, and ρ_{wp} = the correlation of EBV estimated from whole data on the EBV from partial data.

Finally, this procedure was tested on the larger multi-breed population used in the previous Models 14 and 28. In the multi-breed population, the Pearson correlations were 0.98 and 0.02 between EBV from LM and EBV from TM in the whole population and partial populations, respectively. The Pearson correlations were 0.84 and 0.14 between the EBV from LM in the partial population with the EBV from LM in the whole population and between the EBV from TM in the partial population with the EBV from the TM in the whole population. This suggests when all data are used, correlations between EBV obtained from LM and TM are high. The Pearson correlations between whole and partial EBV

estimated using LM were notably higher than those between whole and partial EBV estimated using TM. However, the striking differences in these correlations compared to the statistics reported in the two previous breed populations present some concern about the EBV estimated from the TM approach. The average BIFacc of the validation heifers in the partial dataset were 0 and 0.05 for LM and TM, respectively, and in the whole dataset were 0.06 and 0.07 for LM and TM, respectively. This is consistent with the importance of HP records to achieve meaningful prediction accuracy. However, the average accuracy was similar between LM and TM when all data were used in the whole population, indicating there was no major increase in prediction accuracy due to using TM compared to LM.

Figure 4.6 presents the estimates for cross-validation procedures in the multi-breed population. The estimates for μ_{wp} were 0.002 and 0.09 for LM and TM, respectively, indicating that both evaluation methods were overestimating genetic differences, albeit TM to a greater extent. The estimates for b_{wp} were 0.36 and 0.01 for LM and TM, respectively, indicating both evaluation methods had strong evidence of dispersion. With an ideal value of 1, the b_{wp} estimate obtained from the LM method was more desirable than the estimate obtained from the TM method, but perhaps this indicates a problem in the fit of the model. This series of partial and whole runs were based on models 14 and 28, where all breed proportions, RHV, YAGE, and CG, were fit. However, with little meaningful differences due to breed type, perhaps this is the cause for the disparity in cross-validation estimates. The estimate for b_{pw} using LM was 1.18 with an expected value of 0, and for TM was 0.44 with an expected value of 0.84, indicating large levels of disparity in the relative increase of prediction accuracy from both evaluation methods. Finally, the ρ_{wp} estimates for LM and TM were 0.65 and 0.058, respectively, indicating the correlations were undesirable for both evaluation methods, but particularly for the TM evaluation. The reason is EBV produced from the whole dataset were totally uncorrelated with the EBV produced from the partial run of the TM evaluation. This introduces concern for the evaluation method, and draws attention to possible issues with model fit. The partial runs were evaluated using the !BLUP 3 qualifier which ignored estimating variance components and instead simply calculates the fixed and random effects. Models are

rarely correct, and in the case of this multi-breed population the various breed differences were accounted for as fixed effects (Quaas, 1987), which is rarely done and can be biased as breeds have divergent genetic selection (Kennedy, 1991). It is possible that this method of estimating EBV lacked the precision of estimating EBV on such a large population using TM methodology. Regardless, these results introduce concern for both the validity of LM and TM evaluation methods if the cross-validation results are reliable. Both LM and TM evaluation methods showed evidence of bias and dispersion and were inconsistent with the cross-validation procedures estimated in the previous independent breed populations.

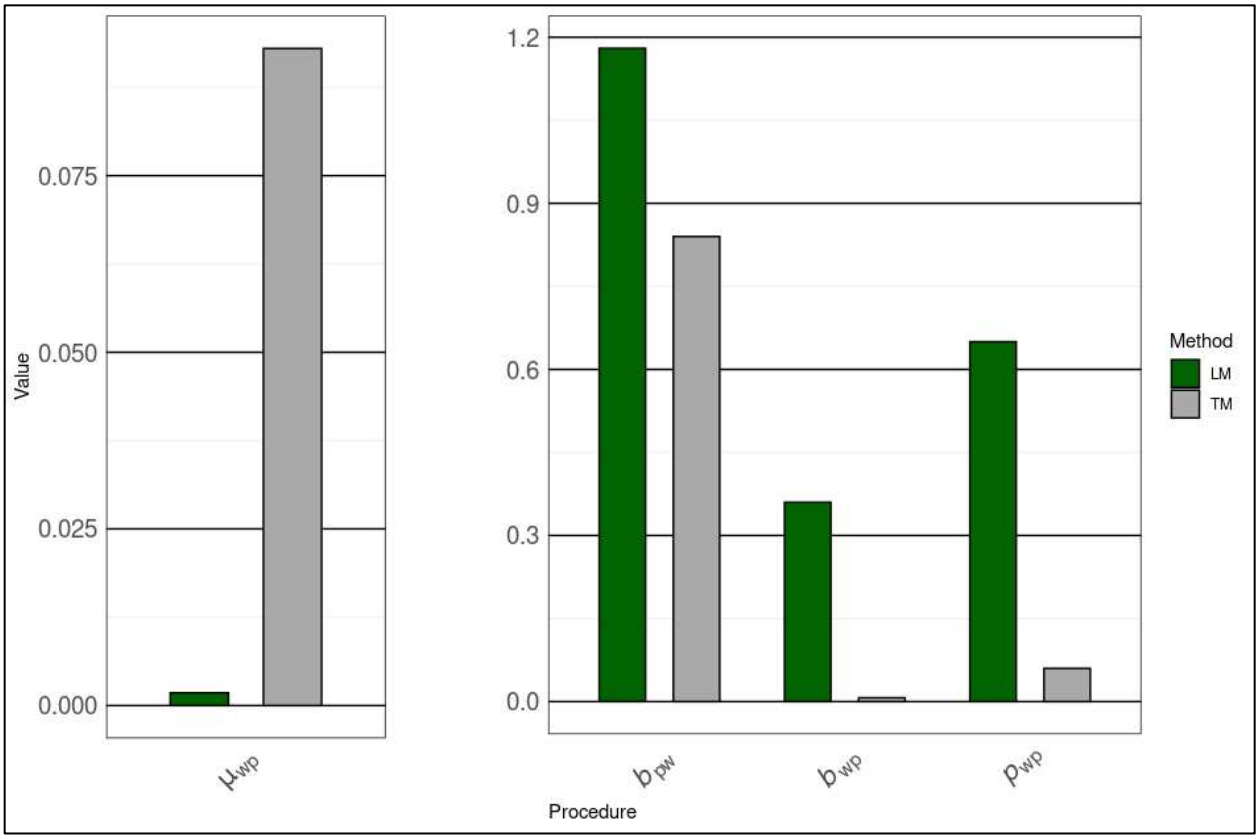

Figure 4.6. Estimates of validation statistics comparing linear models (LM) and threshold models (TM) for the prediction of heifer pregnancy (HP) in a multi-breed population of heifers.

* Where μ_{wp} = the difference in means of EBV estimated from whole data and EBV estimated from partial data evaluations, b_{pw} = the regression of EBV estimated from the partial data on the EBV from the whole data evaluations, b_{wp} = the regression of EBV estimated from whole data on EBV from the partial data evaluation, and ρ_{wp} = the correlation of EBV estimated from whole data on the EBV from partial data.

4.4 Conclusion

This study compared the prediction of HP using LM and TM methods and estimated specific effects for heterosis and breed differences. The results support previous literature claims that greater heritability can be explained by observing HP on the underlying scale. It's clear that TM for the evaluation of heifer pregnancy HP are viable and have been appropriately developed in the industry, and despite the trait being lowly heritable, producers can still achieve genetic progress through selection. This study also established breed differences and the influence of heterosis on HP as is necessary for multi-breed genetic evaluation. While some breed differences were statistically significant, most breed solutions were not meaningful, suggesting that breeders can use diverse breeds in composite development without detriment to HP. This was not the case with heterosis however, for in herds where heifer fertility is a concern, crossbreeding offers the fastest path to meaningful improvements due to the advantages of heterosis as a factor in HP. Ultimately, producers should prioritize effective management practices, including crossbreeding, alongside their breeding strategies to ensure long-term success in improving fertility rates.

When it comes to genetic evaluation however, due to the challenges with ECP, high pregnancy rates in most populations resulting in a lack of variation, and the lack of support for single step genomic evaluation of TM using BOLT software, a secondary goal of this paper was to compare estimates of bias, dispersion and prediction accuracy of the competing LM and TM evaluation methods. These results showed that LM and TM may be evaluating HP equally. In independent Red Angus and Simmental evaluations, no one genetic evaluation method had an advantage in prediction accuracy, with little evidence of bias and dispersion in the breeding values predicted. While results from the multi-breed population cross-validation procedure were mixed, there was little indicator that TM was improved over LM and vice versa.

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CHAPTER 5 - GENETIC PARAMETER ESTIMATES FOR AGE AT FIRST CALVING IN MULTIPLE BREED POPULATIONS AS A PROTOTYPE GENETIC EVALUATION TO SELECT FOR EARLIER CALVING IN BEEF HEIFERS

Summary

The ability to identify heifers that may calve earlier has major economic consequences. Heifers that calve earlier have been shown to have higher rebreeding rates and wean heavier calves with greater lifetime fertility and longevity. Earlier calving heifers have a greater opportunity to regain an optimal body condition, which leads to improved rates of subsequent breeding. Heifers that do not calve as a 2-year-old or fail to rebreed represent an economic loss for producers. Age at first calving (AFC) is a relatively simple phenotype to collect, as it is simply the difference in days between a heifer's date of birth and the date of birth of her first progeny. Many examples of variance component estimation of AFC exist in literature, particularly in the dairy industry. Despite the economic importance of the trait, no examples of a successful genetic evaluation exist to identify heifers that calve earlier in life. As a result of the lack of expected progeny differences for early calving (AFC), the objective of this study was to investigate the genetic control of AFC in a multi-breed population of beef heifers. Heifer pregnancy data were obtained from International Genetic Solutions, where females with exposure records were included in the population. Models were implemented using single-breed populations and then combined into a larger multi-breed population so heterosis and breed effects could be estimated. Females with a calving record between 630 and 810 days were included in the analysis. Females with embryo transfer or multiple birth progeny were excluded. Records from single-animal contemporary groups (CG), CG with no variation, and CG with less than 5 animals were eliminated. After data filtering, there were 149,379 Simmental with a mean Simmental breed proportion of 0.58 ± 0.25 and 83,191 Red Angus records with a mean Red Angus breed proportion of 0.80 ± 0.13. A 3-generation pedigree file containing 291,530 Simmental animals with 25,585 unique sires and 161,921 unique dams with a mean inbreeding value of

0.020, and a 3-generation pedigree file containing 174,914 Red Angus animals with 19,733 unique sires and 99,464 unique dams with a mean inbreeding value of 0.019 were used for separate analysis. The mean AFC in Simmental and Red Angus was 724.8 ± 28.64 d, and 724.2 ± 29.93 d, respectively. Data for each breed were modeled separately using a single trait animal model with random additive genetic and residual effects and the fixed effect of contemporary group using ASReml 3.0. Contemporary group was defined as breeder, herd, year born, birth group, and yearling group. The additive, residual, and phenotypic variances for Simmental were 120.08, 520.37, and 640.45 d^2, respectively. For Red Angus, 85.67, 543.56, and 629.24 d^2 were the additive, residual, and phenotypic variances, respectively. The heritability estimates of AFC for Simmental and Red Angus were 0.19 ± 0.01 and 0.14 ± 0.01, respectively. These results demonstrate AFC in days is lowly to moderately heritable. Lower residual and higher additive variance in Simmental compared to Red Angus may suggest the Simmental population has greater variation for underlying fertility influences such as age at puberty. However, when evaluating the genetic trend for both breeds the results seemed incongruous as AFC was sharply increasing over time. Many beef producers mass mate heifers at a single fixed breeding date. As a result, older heifers in a CG will not have the ability to have a younger AFC compared their younger counterparts in the same CG if conception occurs on the same day. To account for this systematic management influence which may be creating a disadvantage in some heifers, age differential (DIFF) was included to account for age differences prior to first exposure and was defined as the difference in days between an individual's birth date and the earliest birth date of an animal in a defined contemporary group. In addition to including DIFF as a fixed effect, accounting for heifer body weight prior to breeding was also considered, and subsequent bivariate animal models of AFC that included yearling weight (YW) were performed. After data filtering, there were 149,350 calving records. A 3-generation pedigree file was used containing 365,637 animals, with 37,420 unique sires and 219,533 unique dams with a mean inbreeding value of 0.021. Two bivariate multi-trait animal models for AFC and YW with random additive genetic and residual effects and fixed effects of contemporary group, breed proportion, and retained hybrid vigor were used. The first model consisted of the aforementioned effects, while the second model included DIFF as

an additional fixed effect. Analyses were performed using ASReml 3.0. When DIFF was not included as a fixed effect, the additive, residual, and phenotypic variances for AFC were 126.1, 456.8, and 582.9 d^2, respectively, and the genetic correlation between AFC and YW was 0.36 ± 0.02. When DIFF was included as a fixed effect, the additive, residual, and phenotypic variances for AFC were 10.0, 326.0, and 336.0 d^2, respectively. The genetic correlation between AFC and YW was 0.19 ± 0.04. In the absence of DIFF, the heritability estimates for AFC and YW were 0.22 ± 0.01 and 0.44 ± 0.01, respectively, but were 0.03 ± 0.003 and 0.44 ± 0.01 respectively, when DIFF was included. Age differential had a significant effect on AFC at –0.86 ($P < 0.0001$). The low additive genetic variance of AFC, when accounting for DIFF, suggests that the influence of a female's age going into a fixed breeding date explains much of the variation in AFC. Because of how beef producers manage their heifers, and few beef animals are ever first exposed at the onset of puberty, it can be determined AFC is a biased observation for earlier calving. The low heritability estimate for AFC and low genetic correlation with YW suggests that selection for improved AFC is dependent on producers' management practices to ensure females calve earlier in a calving season.

5.1 Introduction

The ability of a heifer to calve earlier in a breeding season has major implications on the economic success of heifers in a production system. Replacement heifers are a significant expenditure for beef producers as there is a significant cost to develop heifers to reach an appropriate body weight prior to pregnancy (Clark et al., 2005); therefore, heifers that fail to breed represent a lost investment because infertility is a primary reason for culling (USDA, 2010). A secondary concern of replacement heifer development is ensuring heifers calve earlier in a calving season. Age at first calving (AFC) is a critical element to heifer rebreeding success and can influence the overall lifetime profitability of an animal in a herd (French et al., 2013). Heifers with greater body weight before initial breeding have higher pregnancy rates, and females that calve earlier in a calving window produce heavier calves at weaning and are

cycling at a higher rate at the beginning of the next breeding season compared to later-calving contemporaries (Funston et al., 2012).

Several studies have investigated the genetic component of age at first calving (Gutierrez et al., 2002; Bormann and Wilson, 2010; Berry et al., 2014; Brzakova et al., 2020; Pardo et al., 2020; Gonzalez –Murray et al., 2021); and typical of most fertility traits, age at first calving (AFC) is reported as a lowly heritable trait (0.08-0.37). As a lowly heritable trait, there are numerous extraneous influences that may impact the age when a heifer has her first calf, such as her age at first exposure, first service conception rate, gestation length, breed, heterosis, age at puberty, body condition score, and body weight.

Age at first calving is a simple trait to collect as it only requires birth dates to determine the phenotype, which is simply the difference in days between a heifer's birth date and her first progeny. This means that AFC encompasses pubertal age, conception rate at either AI or natural services in a breeding season, and gestation length of an individual. Age at first calving is considered a cheap and easy phenotype to measure but may lack the precision necessary for large-scale genetic evaluation and genetic improvement. Virtually no beef production systems expose heifers at the onset of puberty, and instead, they rely on fixed breeding seasons to provide opportunities for pregnancy. Thus, the expression of AFC is predicated upon the initial date of first exposure and the length of the breeding season. Heifers that are born later in a calving season and are therefore younger in their cohort at first exposure would have more opportunity to have a younger AFC, and heifers that are born earlier in a calving season would be older than their contemporaries at first exposure and therefore have less opportunity for younger AFC (Bormann et al., 2010).

There are no examples of commercially available genetic evaluations of AFC in North American *Bos taurus* breeds of cattle. Potential reasons for this could be attributed to the differences in breeding season variability and differing lengths of calving windows could prove challenging to properly account for in a genetic model. This, in addition to heifers that fail to conceive at 2 years of age, means there will be no observation for AFC, and these animals will not be included in any evaluation for the trait. This suggests that AFC is limited in its capability to predict actual fertility compared to genetic evaluations of

the more economically relevant trait, heifer pregnancy. Though the ability to predict and select heifers with an improved ability to calve earlier in a calving window would allow producers to better select replacement heifers and maximize the economic efficiency of replacement heifer development and improve cow lifetime profitability. As a step toward developing tools to improve AFC, this study examined the genetic parameters of AFC in multiple breed populations of beef heifers.

5.2 Materials and Methods

Data used in this study were obtained from an existing database, and as such, an Institutional Animal Care and Use Committee (IACUC) approval was not required.

5.2.1 Data collection and description

Data were obtained from a historical database from the American Simmental Association (ASA) and International Genetic Solutions (IGS) genetic evaluation. The IGS genetic evaluation combines data from over 20 beef breed associations globally into a single multi-breed genetic evaluation. As of the writing of this manuscript, there are no genetic prediction tools for heifer fertility related traits in the IGS multi-breed genetic evaluation. Heifer exposure and pregnancy data (n=740,423) were retrieved in February 2021 from IGS. There were 9 beef breed associations contributing heifer exposure and pregnancy data for this study (Table 4.1). In addition, a performance data file including animal ID, breeder ID, herd ID, birth code, birth contemporary group, weaning management, weaning pasture, weaning contemporary group, yearling feed unit, yearling contemporary group, serial birth date, serial weaning date, serial yearling date, birth weight, weaning weight, yearling weight, age of dam, sex, and calving ease code were retrieved on all animals and progeny in the study.

In the initial group, heifers were required to have a successful heifer exposure code (Yes = 1) to be included in the study. This approach allowed the population to be narrowed to a more manageable group for timeliness of parameter estimation and helped eliminate potential heifers not exposed as yearlings that would have extreme AFC observations if they first calved as 3-year-olds. Age at first calving was defined as the difference in days from heifer serial birth date and her first calf's serial birth

date. After eliminating extreme negative/erroneous values (e.g. calf was born before dam issue), the minimum, mean, maximum, and standard deviation of raw AFC were 0 d, 761.14 d, 4,436 d, and 100.71 d, respectively. A minimum value of 0 has to do with data integrity issues from producers or breed associations misreporting birth dates. However, out of 647,539 preadjusted records there were only 73,357 records less than 200 days. Ultimately, this highlights an inherent challenge with large national cattle evaluation (NCE) databases, where a cow might not be registered until she has had her first calf at 12, though the producer still reported a heifer exposure and pregnancy record. Establishing an appropriate threshold on phenotypic age ranges is crucial for evaluation integrity. For this reason, records were limited to females calving between 630 and 810 days of age to remove extreme cases. Females with embryo transfer or multiple birth progeny were removed from the study. Contemporary group (CG) was defined as a concatenation of breeder ID, herd ID, birth year, birth contemporary group, weaning contemporary group, and yearling contemporary group (same CG definition used in all IGS yearling age traits). Records from single-animal contemporary groups, and CG with no variation were removed from the study. There were 11,363 unique CG, with an average CG size of 24.9 animals. After data filtering, there were 284,032 AFC records. A three–generation pedigree file containing 55,313 unique sires and 359,390 unique dams was also retrieved. Figure 5.1 provides a histogram of the count of heifer AFC records across the age range.

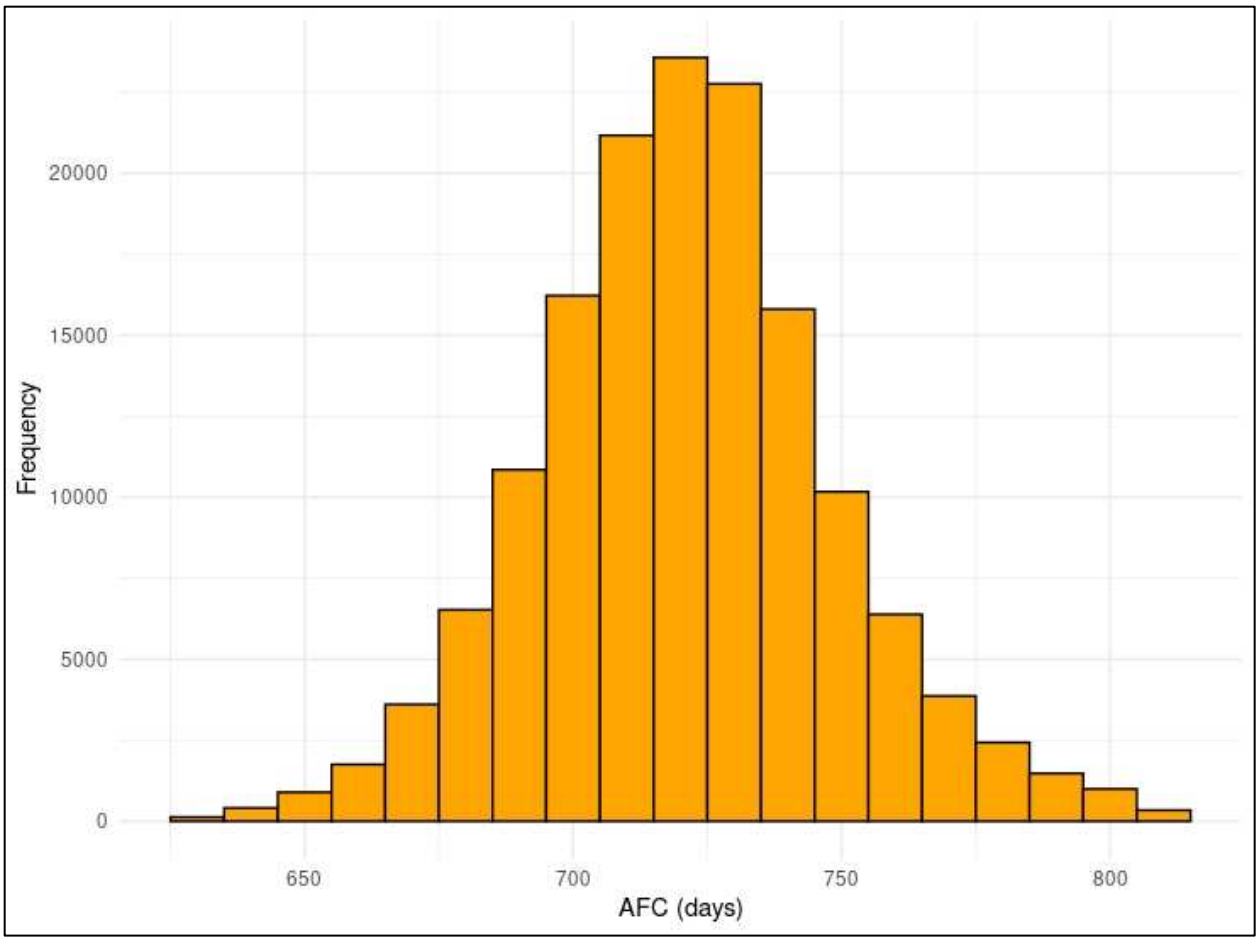

Figure 5.1. Distribution of heifer age at first calving (AFC) observations in a multi-breed population of beef heifers (n=149,350).

A second group of animals without the requirement for initially being exposed was established. Since exposure and pregnancy observations are not always necessary to establish an AFC phenotype, and instead simple birth date and calving records can accomplish AFC phenotype creation, historical records from the Red Angus Association of America and the American Simmental Association breed registries were used for a secondary subsequent analysis. Performance and pedigree files of the entire breed registry were retrieved, and AFC was determined as the difference in days between a heifer's serial birth date and the birth date of her first registered progeny. The same calving record window of 630 to 810 days of age was used and females with embryo transfer and multiple birth progeny were removed. Records from single-animal CG, CG with no variation, and CG that had less than 5 animals were removed. After data

filtering, there were 149,379 Simmental, and 83,191 Red Angus records. A 3-generation pedigree file containing 291,530 Simmental animals with 25,585 unique sires and 161,921 unique dams, and a 3-generation pedigree file containing 174,914 Red Angus animals with 19,733 unique sires and 99,464 unique dams were used for separate breed population AFC analysis.

As a result, there are three separate populations used in this study; the multi-breed population with data derived from heifer exposure/pregnancy records, the Red Angus population derived from registry data, and the Simmental population derived from registry data, both of which are also included in the multi-breed population.

5.2.2 Fixed and random effects

There are numerous factors influencing AFC, such as breed, heterosis, and age at breeding. Still, none of these have been summarized by the Beef Improvement Federation (BIF) because of a lack of development for the trait in North American beef cattle breeds, and as a result, this study aimed to investigate relevant fixed effects for AFC. To determine the significance of proposed factors, incremental Wald F-tests were conducted simultaneously with variance component estimation using the statistical software package ASREML 3.0 (Gilmour et al., 2009) as outlined in Equation 4.1 and again below:

$$W = [\hat{\theta} - \theta]^{-1} [Var(\hat{\theta})]^{-1} [\hat{\theta} - \theta]$$

where $\hat{\theta}$ represents the maximizing argument of an unconstrained likelihood function or the maximum likelihood estimate obtained when all potential explanatory variables were included in the model. "Var" denotes the variance, and θ corresponds to the hypothesized maximum likelihood estimate under the assumption that the null hypothesis is true (H_0: $\theta_k = 0$), which assumes that the k_{th} parameter does not help to explain variation in the response variable. The incremental Wald F-test statistics have an asymptotic χ^2 distribution with degrees of freedom given by the number of estimable effects (n-k) that are adjusted using the Kenward-Roger method (Kenward and Roger, 1997). For balanced designs, the Wald F-statistics are numerically identical to F-statistics obtained from standard analysis of variance.

With 9 breed associations contributing data to this multi-breed study and numerous composites representing many breeds in each population, breed differences were investigated as important factors influencing AFC. The pedigree file obtained from IGS contained individual breed proportions for Simmental, Angus, Hereford, Brahman/Zebu, Gelbvieh, Limousin, Chianina, Maine-Anjou, Shorthorn, Red Angus, Salers, South Devon, Charolais, Holstein, Jersey, Other American, Other British, Other Continental, Other Dairy, and Other or Unknown. Breed groups were consolidated to avoid overfitting the model. As a result, all dairy breeds were combined into a single breed proportion (DAIRY), all *Bos indicus* influenced animals were combined (IND), Salers, Charolais, Maine-Anjou and Other Continental were combined (OCONT). South Devon, Hereford, Shorthorn Other Unknown, and Other English were combined (OENGL). Other Unknown was combined into the Other English under the assumption that the Angus breed is the most prevalent breed in the industry and thus, the most likely breed influence when the actual breed was unknown. This resulted in breed categories of Simmental (SIM), Black Angus (ANG), Gelbvieh (GBV), Limousin (LIM), Red Angus (RED), IND, DAIRY, OCONT, and OENGL. In subsequent models, individual breed groups of SIM, ANG, GBV, LIM, and RED were then consolidated into all Continental breeds (CONT), and all English breeds (ENGL). Breed proportion was represented as a value from 0 to 1, and when all breed groups were summed were equal to 1.

Table 5.1. Summary statistics for age at first calving (AFC), breed proportion, and retained hybrid vigor (RHV) in a multi-breed population of heifers*.

Effect	n	Min	Mean	Max	Var	Sd
AFC (d)	284,032	630	722.01	810	811.25	28.48
RHV (∝)	277,953	0	0.44	1.0	0.06	0.24
∝ Angus	284,032	0	0.21	1.0	0.05	0.22
∝ Red Angus	284,032	0	0.19	1.0	0.11	0.33
∝ Simmental	284,032	0	0.23	1.0	0.10	0.32
∝ Limousin	284,032	0	0.16	1.0	0.11	0.34
∝ Gelbvieh	284,032	0	0.09	1.0	0.04	0.20
∝ Indicus-Influenced	284,032	0	0.002	0.54	0.0004	0.02
∝ Dairy	284,032	0	0.002	0.57	0.0002	0.01
∝ Other English	284,032	0	0.02	1.0	0.004	0.07
∝ Other Continental	284,032	0	0.004	0.996	0.0004	0.02
∝ Other Unknown	284,032	0	0.08	1.0	0.03	0.16

* Heifers were limited to those initially indicated as being exposed as a yearling.
** ∝ = Proportion

Diverse breed and composite representation in this population necessitates the need to investigate the influence of heterosis on AFC. Since breed proportions of sires and dams were known, proportion of individual retained hybrid vigor (RHV) was used as an estimate of the degree of heterosis in individual animals and is expressed as a value ranging from 0 to 1. Summary statistics for AFC, breed proportions and RHV are described in Table 5.1. Since the F1 hybrid vigor value is unknown and we are less interested in predicting the achieved hybrid vigor in performance, rather understanding the effect of hybrid vigor on AFC, a version of the RHV equation that does not include the typical F_1 hybrid vigor for a trait is used. The formula used to estimate RHV was modified from the set of equations presented by Bourdon (2000) and was outlined in equation 4.2 and again below:

$$\widehat{RHV} = (1 - \sum_{i=1}^{n} p_{s_i} p_{d_i})$$

where p_{si} is the proportion of breed *i* in the sires, p_{di} is the proportion of breed *i* in the dams and n is the total number of breeds involved. In expanded form, the formula appears as:

$$\widehat{RHV} = (1 - (p_{s_1}p_{d_1} + p_{s_2}p_{d_2} + p_{s_3}p_{d_3} + \cdots + p_{s_n}p_{d_n}))$$

Because few, if any, beef producers expose heifers at the onset of puberty, differences in heifer age at the beginning of fixed breeding dates was a necessary fixed effect to account for. Retained heifers are typically managed as a group and then bred using fixed-time AI or exposed to a natural service sire(s), so that the onset of breeding is fixed. Conception occurs randomly in pasture-exposure because it depends on heifers being in estrus when a healthy and fertile sire is nearby. The expression of AFC is predicated upon the initial date of first exposure and the length of the breeding season, and as such heifers that are born later in a calving season and are therefore younger compared to their older heifer contemporaries would have a greater ability to have a younger AFC. This concept was not generally discussed or accounted for in literature encompassing evaluations of AFC. The reason is that many of the literature studies were primarily on dairy animals where this assumption may not hold true, as many dairy operators prefer to expose young dairy heifers shortly after puberty has been reached (Gill et al., 1976; Haworth et al., 2008; Heise et al., 2018; Stefani et al., 2021). In the initial stages of this investigation, differences in age prior to a fixed first exposure was not considered, and preliminary results seemed incongruous. To account for this factor, an age differential was determined. Age differential (DIFF) was defined as the difference in days between an individual's birth date and the earliest birth date of an animal in their defined CG. Therefore, the oldest heifer in a CG would have a DIFF of 0. Heifers with a DIFF greater than 100 were excluded. To compare the potential impact of age differences relative to the start of a breeding season, two separate models were performed on the same multibreed population with the same fixed effects of CG, breed proportion and RHV; however, one model included DIFF, and the other did not.

A priori heifer body weight and body condition are important factors related to heifer fertility. Because exposure happens relatively close to yearling age, and yearling weights were generally known in all populations, two models included yearling weight (YW) as an additional trait in bivariate linear animal models in the multi-breed population. However, body condition score was not commonly reported on all three populations and generally lacks variability in heifer populations so was not included as a fixed or random effect in this study. Heifers that did not have a YW phenotype were removed from the analysis

and after data filtering there were 149,350 heifers in the multi-breed population. The 3-generation pedigree file had 37,420 unique sires, and 219,533 unique dams. Summary statistics for AFC, YW, DIFF, breed proportion, and RHV are described in Table 5.2.

Table 5.2. Summary statistics for age at first calving (AFC), yearling weight (YW), age differential (DIFF), breed proportion, and retained hybrid vigor (RHV) in a multi-breed population* of heifers.

Effect	n	Min	Mean	Max	Var	Sd
AFC (d)	149,350	630	721.45	810	760.14	27.57
YW (lbs)	149,350	350	830.12	1550	14,595.22	120.81
DIFF (d)	141,456	0	26.89	100	413.96	20.35
RHV (∝)	148,022	0	0.41	1.0	0.054	0.23
∝ English	149,350	0	0.48	1.0	0.16	0.39
∝ Continental	149,350	0	0.45	1.0	0.13	0.36
∝ Indicus-Influenced	149,350	0	0.001	0.54	0.0004	0.02
∝ Dairy	149,350	0	0.002	0.57	0.0002	0.01
∝ Other Unknown	149,350	0	0.07	0.94	0.02	0.15

* Heifers were limited to those that had both AFC and YW observations. Being initially reported as exposed was not a requirement.
** ∝ = Proportion

5.2.3 Animal models for Age at First Calving

Because AFC is a continuous variable, a linear animal model was the most appropriate model choice for BLUP and variance component estimation. A linear model was used for three populations described above as the Simmental, Red Angus, and multi-breed populations. The model equation (5.1) in matrix form was:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Zu} + \boldsymbol{e} \qquad \text{Eq. 5.1}$$

where $\boldsymbol{y}$ was a vector of AFC observations, $\mathbf{X}$ was a known incidence matrix relating observations in $\boldsymbol{y}$ to fixed effects, $\boldsymbol{b}$ was a vector of unknown solutions for fixed effects including CG, breed proportion, and RHV, $\mathbf{Z}$ was an incidence matrix relating observations in $\boldsymbol{y}$ to random animal effects, $\boldsymbol{u}$ is a vector of random animal effects for AFC, and $\boldsymbol{e}$ was a vector of random residuals. It was assumed that residual

effects, including random environmental and non-additive genetic effects are independently distributed with variance σ_e^2, so that $var(e) = I\sigma_e^2 = R$; $var(u) = A\sigma_a^2 = G$, and $cov(u, e) = 0$, where **A** was the Wright's numerator relationship matrix. A bivariate animal model was also used for heifers where YW phenotypes were known. The bivariate animal model in matrix form is described in the following equation (5.2):

$$\begin{bmatrix} Y_{AFC} \\ Y_{YW} \end{bmatrix} = \begin{bmatrix} X_{AFC} & 0 \\ 0 & X_{YW} \end{bmatrix} \begin{bmatrix} b_{AFC} \\ b_{YW} \end{bmatrix} + \begin{bmatrix} Z_{AFC} & 0 \\ 0 & Z_{YW} \end{bmatrix} \begin{bmatrix} u_{AFC} \\ u_{YW} \end{bmatrix} + \begin{bmatrix} e_{AFC} \\ e_{YW} \end{bmatrix} \quad \text{Eq. 5.2}$$

where Y_i was a vector of observations for AFC and YW, X_i was an incidence matrix relating observations to fixed effects including; CG, RHV, breed proportion (grouped by British, Continental, Indicus-Influenced, Dairy, and Other), and in one model DIFF, b_i was a vector of unknown fixed effect solutions, Z_i was an incidence matrix relating AFC and YW observations in y to random additive genetic effects, u_i was a vector of random additive genetic effect solutions, and e_i was a vector of random residuals. With a random additive (co)variance matrix of:

$$var \begin{bmatrix} u_{AFC} \\ u_{YW} \end{bmatrix} = \begin{bmatrix} \sigma^2_{a_{AFC}} & \sigma_{a_{AFC},a_{YW}} \\ \sigma_{a_{YW},a_{AFC}} & \sigma^2_{a_{YW}} \end{bmatrix} \otimes A$$

where $\sigma^2_{a_{AFC}}$ represented the additive genetic variance for AFC, $\sigma_{a_{YW},a_{AFC}}$ and $\sigma_{a_{AFC},a_{YW}}$ corresponded to the additive covariances among AFC and YW, and $\sigma^2_{a_{YW}}$ represented the additive genetic variance for YW. In the above, ***A*** represented the Wright's numerator relationship matrix and $\otimes$ indicated the Kronecker product. The (co)variance matrix for the residual effects was described as:

$$var \begin{bmatrix} e_{AFC} \\ e_{YW} \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e_{AFC}} & I\sigma_{e_{AFC},e_{YW}} \\ I\sigma_{e_{YW},e_{AFC}} & I\sigma^2_{e_{YW}} \end{bmatrix}$$

where $\sigma^2_{e_{AFC}}$ represented the residual variance of AFC, $\sigma_{e_{YW},e_{AFC}}$ and $\sigma_{e_{AFC},e_{YW}}$ were the residual covariances between both traits, and $\sigma^2_{e_{YW}}$ represented the residual variance for YW. In this case, ***I*** was an n x n identity matrix, with n being equal to the number of animals since all had an observation for AFC and YW.

5.2.4 Statistical analysis

Data preparation was performed with the Animal Breeder's Tool Kit (ABTK; Golden et al., 1995) package of tools on the Colorado State University Center for Genetic Evaluation of Livestock (CGEL). Variance parameter estimates, breeding values, and fixed effect solutions for 5 separate models were obtained with restricted estimate maximum likelihood (REML) analysis using ASREML3.0 (Gilmour, 2009). Table 5.3 outlines the separate animal models used in this study. Because of a lack of representation, OIND, and OUNK were not included as breed proportions in model 3.

Table 5.3. Description of models used to generate variance parameter estimates, random effect solutions, and fixed effect solutions for age at first calving (AFC) and yearling weight (YW).

Model Name	Population	Model Type	Dependent Variable	Fixed Effects	n
Model 1	Simmental	Linear Animal Model	AFC	CG	149,379
Model 2	Red Angus	Linear Animal Model	AFC	CG	83,191
Model 3	Multi-breed	Linear Animal Model	AFC	CG, RHV, Breed ∝	284,032
Model 4	Multi-breed	Bivariate Linear Animal Model	AFC, YW	CG, RHV, Condensed Breed ∝*	149,350
Model 5	Multi-breed	Bivariate Linear Animal Model	AFC, YW	CG, RHV, Condensed Breed ∝*, DIFF	149,350

* Breeds were condensed into English, Continental, Indicus, and Dairy breed categories.

Breeding values obtained from the solutions of Models 4 and 5 were used to plot genetic trends. The average breeding value for AFC by year of birth was plotted since 1960. Genetic trends were separated into 4 breed categories: All animals, Angus, Red Angus, and Simmental. Trends were plotted using R statistical software v4.1.2 and the GGPLOT2 package.

5.3 Results and Discussion

Only heifers that had exposure and pregnancy observations reported were included in models 1, 2, and 3. The assumption was that records that originate from contemporary groups with exposure and pregnancy reporting are more complete and robust for genetic evaluation purposes. Summary statistics for AFC observations from Models 1-3 are presented in Table 5.4 The minimum and maximums are a result of the bounds applied to AFC.

Table 5.4. Summary statistics for age at first calving (AFC) in Simmental, Red Angus, and combined multi-breed populations of heifers.

Model	Population	Min	Mean	Max	Var (d^2)	sd (d)
Model 1[1]	Simmental	630	724.8	810	820.4	28.6
Model 2[2]	Red Angus	630	724.2	810	854.5	29.2
Model 3[3]	Multi-breed	630	722	810	811.2	28.5

[1] Model 1 = Simmental population fitting CG as the only fixed effect.
[2] Model 2 = Red Angus population fitting CG as the only fixed effect.
[3] Model 3 = Multi-breed population fitting CG, retained hybrid vigor, and breed proportion as fixed effects.

Variance components for Models 1- 3 are presented in Table 5.5. These results are similar to those reported in literature estimates. Frazier et al. (1999) and Toelle and Robinson (1985) reported heritability estimates for AFC of 0.22 in Angus heifers and 0.24 in Hereford heifers, respectively. Pardo et al. (2020) reported average posterior mean estimates of 52.73, 665.70, and 0.08 for AFC direct additive variance (σ_a^2), phenotypic variance (σ_p^2), and heritability (h^2), respectively in a multi-breed population of Angus, Hereford, and crossbred heifers. The three previously mentioned studies and the present study restricted the populations to include heifers that successfully had a calf as a two-year-old. As such, their open contemporaries either had an AFC phenotype outside of the acceptable range or were culled prior to a record of a calf being born and not included in the dataset. Bormann and Wilson (2010) reported genetic parameters for AFC in a population of Angus heifers that were adjusted by considering open heifer contemporaries, where open heifers were given an AFC observation 30, 60, or 90 days after the oldest

AFC record within their CG. In their whole Angus heifer population, the heritability estimates did not differ between the 30, 60, and 90d adjustments, and they reported estimates of 394.43, 1395.17, and 0.28 for σ_a^2, σ_p^2, and h^2 respectively (Bormann and Wilson, 2010). Although h^2 estimates were variable across populations and studies, the results in models 1 and 2 suggest that genetic progress for earlier age at first calving could be achieved in Simmental and Red Angus populations. The lower additive variance and higher environmental variance observed in the primarily Red Angus population Model 2 compared to the Simmental population used in Model 1 suggests that the Simmental population may have greater variation for underlying fertility influences such as age at puberty. To understand this better in the context of the broader beef industry, where many producers are crossbreeding, we accounted for retained hybrid vigor and breed proportions (Table 5.7) in Model 3.

Table 5.5. Genetic parameter estimates for age at first calving (AFC) in a Simmental, Red Angus, and multi-breed population of beef heifers.

Model	n	σ_a^2	σ_e^2	σ_p^2	h^2	*se*
Model 1[1]	149,379	120.08	520.37	640.45	0.188	0.006
Model 2[2]	83,191	85.68	543.57	629.24	0.136	0.008
Model 3[3]	284,032	126.81	490.80	617.61	0.205	0.004

[1] Model 1 = Simmental population fitting CG as the only fixed effect.
[2] Model 2 = Red Angus population fitting CG as the only fixed effect.
[3] Model 3 = Multi-breed population fitting CG, retained hybrid vigor, and breed proportion as fixed effects.

Table 5.6 describes the summary statistics for AFC phenotypes by breed population in model 3. There were no drastic differences in min, mean and max AFC phenotypes across the different breed populations. The mean AFC of all populations was similar to that reported by Frazier et al. (1999); however, they did not exclude observations outside of expected ranges and had minimum AFC observations of 365 d and maximum AFC observations as high as 915 d. The Shorthorn USA (BSHUSA) population had the highest AFC variance (1,017.34 d^2). There was only one representative animal in the

Australian Angus (AANAUS) population, and, as such, had the lowest AFC variance. The breed population in the present study was designated by the breed association where the animal was originally registered. There were situations where multiple breed populations might be represented in a single contemporary group because a breeder may register some animals at numerous breed registries depending on the breeds used in their breeding program.

Table 5.6. Summary statistics for age at first calving (AFC) by breed population.

Breed *	Count	Min	Mean	Max	Var	Sd
AANAUS	1	710	710	710	0	0
AANUSA	594	644	732.05	806	595.80	24.40
BHHUSA	107	660	718.26	774	500.47	22.37
BSHCAN	90	644	734.86	807	686.62	26.20
BSHUSA	735	630	721.51	810	1017.34	31.90
GVHCAN	2,939	630	716.24	810	803.50	28.35
GVHUSA	51,669	630	714.17	810	778.20	27.90
LIMCAN	6,254	633	734.31	810	806.11	28.39
LIMUSA	47,568	630	725.79	810	907.32	30.12
RANAUS	45	662	711	756	666.91	25.82
RANUSA	58,516	630	722.43	810	791.45	28.13
SIMAUS	513	634	713.32	796	809.28	28.45
SIMUSA	115,001	630	723.23	810	751.99	27.42

* Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022). The combination of breed and country codes describes the different breed populations.

Table 5.7 provides the fixed effect solutions for RHV and breed proportions from model 3 in the present study. Cundiff et al. (1974) described the impact that heterosis and breed effects can have on the reproductive fitness of beef females. They reported a 12.6% improvement in heifers conceiving at first service and an 8.6% improvement in conception per estrus due to heterosis in the crossbred dams (either F1's or crossbred females produced in rotational crossbreeding systems). The ability to conceive at first service and higher conception rates per estrus are expected to be related to heifers calving earlier in their lifetime. However, in a subsequent study, Cundiff et al. (1992) related that heterosis effects did not

interact (P>0.05) with AFC management, where heifers born in 1960 and 1961 were managed to calve as 3-year-olds, and heifers born in 1962 and 1963 were managed to calve as 2-year-olds. In that study, heifers diagnosed as not pregnant after their first breeding season were culled. Hickson et al. (2014) also alluded to heterosis being a non-significant factor in AFC in BeefXDairy cross heifers. We had comparable results in the present study, with RHV having a non-significant estimate of 0.249 (P = 0.11) for AFC. The more relevant findings from model 3 were that significant breed differences were observed for AFC. There were significant differences for changes in AFC due to Angus, Red Angus, Simmental, Limousin, and Gelbvieh breed proportions. The most notable differences were seen when the Limousin breed proportion neared 1.0. There was a +14.67 d (P<0.001) effect in heifer AFC. On the contrary, there was a –4.78 d (P<0.0001) effect in AFC when the Gelbvieh breed proportion was 1.0. Angus and Red Angus breed solutions were similar at +10.83 d (P<0.001) and +9.18 d (P<0.001), respectively. These results suggest that as Gelbvieh breed proportion increases, producers will see a favorable decrease in the AFC. In contrast, breeders that increase the proportion of Angus, Red Angus, or Limousin breeds may see an unfavorable increase in the AFC of their heifers. Breed differences such as these can help producers identify which breeds to introduce into their breeding programs to help improve AFC through breed complementarity.

Table 5.7. Effect solutions and estimates of standard error for retained hybrid vigor (RHV) and breed proportion.

Effect	Solution	Se	P Value
RHV (∝)	0.249	0.348	0.11
∝ Angus	10.83	1.108	<0.001
∝ Red Angus	9.182	1.398	<0.001
∝ Simmental	0.926	1.27	<0.001
∝ Limousin	14.67	1.952	<0.001
∝ Gelbvieh	-4.78	2.065	<0.001
∝ Dairy	-3.65	4.73	0.357
∝ Other English	1.139	1.838	0.671
∝ Other Continental	3.117	2.794	0.267

Bourdon and Brinks (1982) suggested that genetics for growth and reproduction were low but favorably correlated and reported a genetic correlation between AFC and YW of –0.17±0.40. For this reason and the importance of heifer body weight and condition on reproduction (Osoro and Wright, 1992), YW was added as a dependent variable to bivariate animal models 4 and 5 in the present study. Additionally, AFC can be limited by when heifers are born and the start of a breeding season. Beef heifers born later in a contemporary group will have a greater opportunity to have a younger AFC (Bormann and Wilson, 2010). Many beef producers do not immediately expose heifers at the onset of puberty; instead, they wait until most females have all reached puberty and will expose them when seasonally appropriate. These defined breeding seasons have a fixed day of first exposure, and it is assumed that all heifers in a contemporary group were first exposed on the same day unless indicated otherwise. Many sources in literature do not account for differences in heifer age prior to exposure when estimating variance components for AFC (Frazier et al., 1999; Gutierrez et al., 2002; Bormann et al., 2010; Berry et al., 2014; Brzakova et al., 2020; Pardo et al., 2020; Gonzalez-Murray et al., 2021), which could explain why heritability estimates were considered over-estimated compared to the same trait in some dairy populations. The reason is that many dairy operators may expose young heifers individually via AI soon after they reach puberty which helps offset the developmental costs incurred in the 2 years before a diary heifer is producing milk (Pursley et al., 1997; Rivera et al., 2004; Fricke, 2019). The individual insemination of heifers in dairy systems rather than the mass-mate exposure style seen in beef systems may be the difference in an explanation of genetic variability for AFC between species. To account for age differences between heifers going into a fixed exposure date, DIFF was included as an age covariate in model 5. Variance components derived from models 4 and 5 were compared in Table 5.8.

Table 5.8. Genetic parameter estimates for age at first calving (AFC) and yearling weight (YW) in a multi-breed population of beef heifers when accounting for age differences prior to first exposure.

Model	Trait	n	σ_a^2	σ_e^2	σ_p^2	h^2	r_g
Model 4[1]	AFC	149,350	126.15	456.79	582.93	0.216±0.006	0.36±0.02
	YW		2,325.74	3,013.0	5,338.7	0.436±0.007	
Model 5[2]	AFC	149,350	9.98	326.01	336.0	0.029±0.004	0.19±0.04
	YW		1,979.06	2,479.98	4,459.0	0.444±0.008	

[1] Model 4 = Multi-breed, bivariate animal model of YW and AFC not accounting for DIFF.
[2] Model 5 = Multi-breed, bivariate animal model of YW and AFC accounting for DIFF.

When not accounting for DIFF, the variance components and heritability estimate for AFC were similar to those reported in the literature. Frazier et al. (1999) reported an average heritability estimate of 0.22 for AFC, and showed the trait was highly negatively genetically correlated with first calving interval and mature calving interval. Gutierrez et al. (2002) reported an AFC heritability estimate of 0.235 and investigated the genetic relationship of AFC with type traits. While most relationships were not meaningful, they reported genetic correlations between AFC and body depth and AFC and thigh development (dimension of muscle on rear leg) in Asturiana de los Valles cattle of 0.445±0.051 and 0.447±0.067, respectively. This suggests that type traits involving more desirable body dimensions may be unfavorably genetically related to AFC. The genetic correlation between AFC and YW from model 4 (+0.36) was notably different than the estimate of –0.17 reported by Bourdon and Brinks (1982). A positive genetic correlation between AFC and YW is undesirable as heifers with genetics for greater weight performance would also have genetics for later AFC. However, it appears that accounting for age differences at first exposure explains much of the genetic variability for the trait. Unlike dairy systems, beef breeders do not expose heifers at the onset of puberty making the development of an AFC genetic evaluation in beef cattle challenging. The practice of mass mating heifers at a fixed date artificially delays first calving in some animals, meaning the variation in AFC is due to management decisions, not genetic. This would also mean any genetic evaluation that does not account for age differences at first exposure

would be overestimating the expected progeny differences (EPD) as many of the differences would be attributed to genetic differences rather than the management-induced delay in breeding.

The heritability estimate produced from model 5 is drastically lower than estimates in literature not accounting for age differences, and the genetic correlation between AFC and YW is closer to 0 in model 5 compared to model 4. Smith et al. (1989) acknowledged that when accounting for heifer day of birth in an AFC prediction model, the birthdate can almost wholly explain the AFC trait. Martinez-Velazquez et al. (2003) accounted for month of birth and age at puberty in an AFC model and reported a direct heritability of 0.08(±0.04) and a maternal heritability of 0. The heritability estimate for AFC when including DIFF in model 5 was 0.029±0.004, suggesting there is little opportunity to improve AFC with genetic selection, but rather efforts should instead be directed towards improving the management of heifers to conceive earlier. This could include exposing heifers shortly after they have reached puberty, but this would be challenging to adopt in many beef systems. Accounting for DIFF in model 5 explained a large amount of the additive genetic variance in AFC. Table 5.9 displays the fixed effect solutions for model 5.

Table 5.9. Fixed effect solutions for a bivariate animal model for age at first calving (AFC) and yearling weight (YW) when accounting for age differences in a contemporary group prior to first exposure.

Effect	Solution	Se	P Value
DIFF (d)	-0.861	-0.86	<0.001
RHV (∝)	-2.511	-2.51	<0.001
∝ Continental	1.660	1.66	<0.001
∝ English	1.935	1.93	0.637
∝ Indicus-Influenced	15.55	4.86	0.006
∝ Dairy	-0.058	4.99	0.008

In model 5 DIFF was highly significant (P<0.001) and suggested that for every 1 day increase in age from the oldest heifer in a contemporary group, led to a -0.86 d lower AFC. This almost wholly accounts for AFC differences. There were also significant breed and heterosis effects in model 5. Heterosis was significantly related to AFC, with results suggesting an animal that neared 100% RHV

would have a –2.511 d lower AFC compared to animals with zero RHV. The only non-significant (P<0.05) breed difference was ENG. However, CONT, IND, and DAIRY were all significant, with IND having a +15.6 d effect on AFC and Dairy having a –0.06 d effect on AFC. This suggests that *Bos indicus* influenced animals are later maturing and, as a result, have higher AFC compared to only English or Continental influenced heifers. Despite having limited dairy influenced animals in this study, the negative solution for DAIRY may be explained by the selection pressure many dairy operations employ to ensure heifers are exposed and pregnant as early as possible. These results are consistent with those reported by Hickson et al. (2014), that suggested beefXdairy cows had production advantages over some straight-bred beef cows due to heterosis and breed differences.

Genetic trends for Angus, Red Angus, Simmental, and all animals were developed using the average breeding value of AFC by year of birth since 1960. Figure 5.2 represents the genetic trends of AFC from breeding values estimated using Model 4, and Figure 5.3 represents the genetic trends of AFC from breeding values estimated from Model 5. It's clear in Figure 5.2 that there is an undesirable increasing trend in AFC that started in the early 2000s and resulted in an approximate 15 d increase in AFC for all breed populations by the year 2022. This linear trend mimics that observed in many YW genetic trends across breed populations. However, when accounting for DIFF in model 5, the genetic trends are not as clear or concerning in Figure 5.3. The Angus population has an AFC trend that has been increasing since the late 1990s, but not of a meaningful magnitude because the difference is less than half a day when DIFF is included in the model. It's clear that accounting for age differences in females prior to their first exposure is necessary because of the management strategies employed by beef producers. For this reason, an AFC evaluation that does not account for DIFF may be inappropriate and misleading for genetic selection.

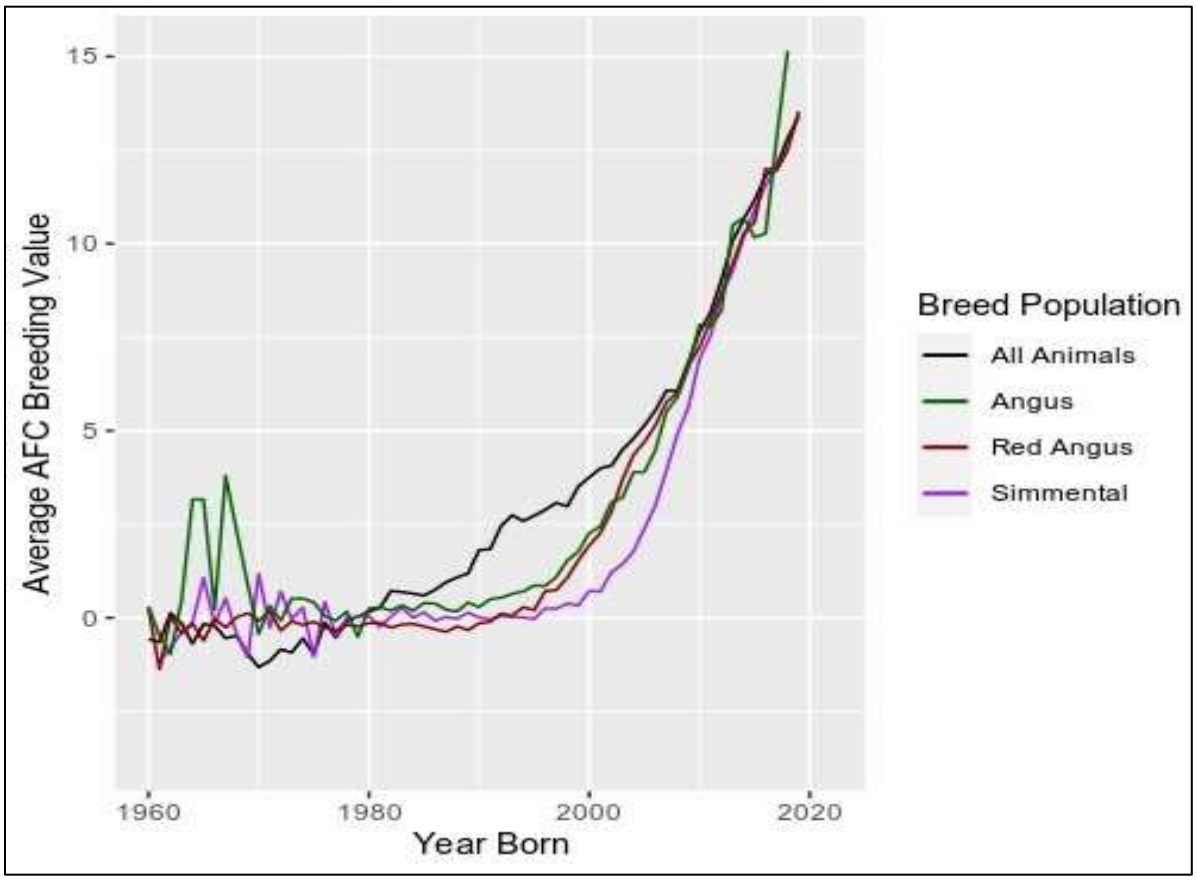

Figure 5.2. Genetic trend for age at first calving (AFC) by year of birth from a bivariate animal model, including yearling weight (YW), when not accounting for age differences prior to first exposure.

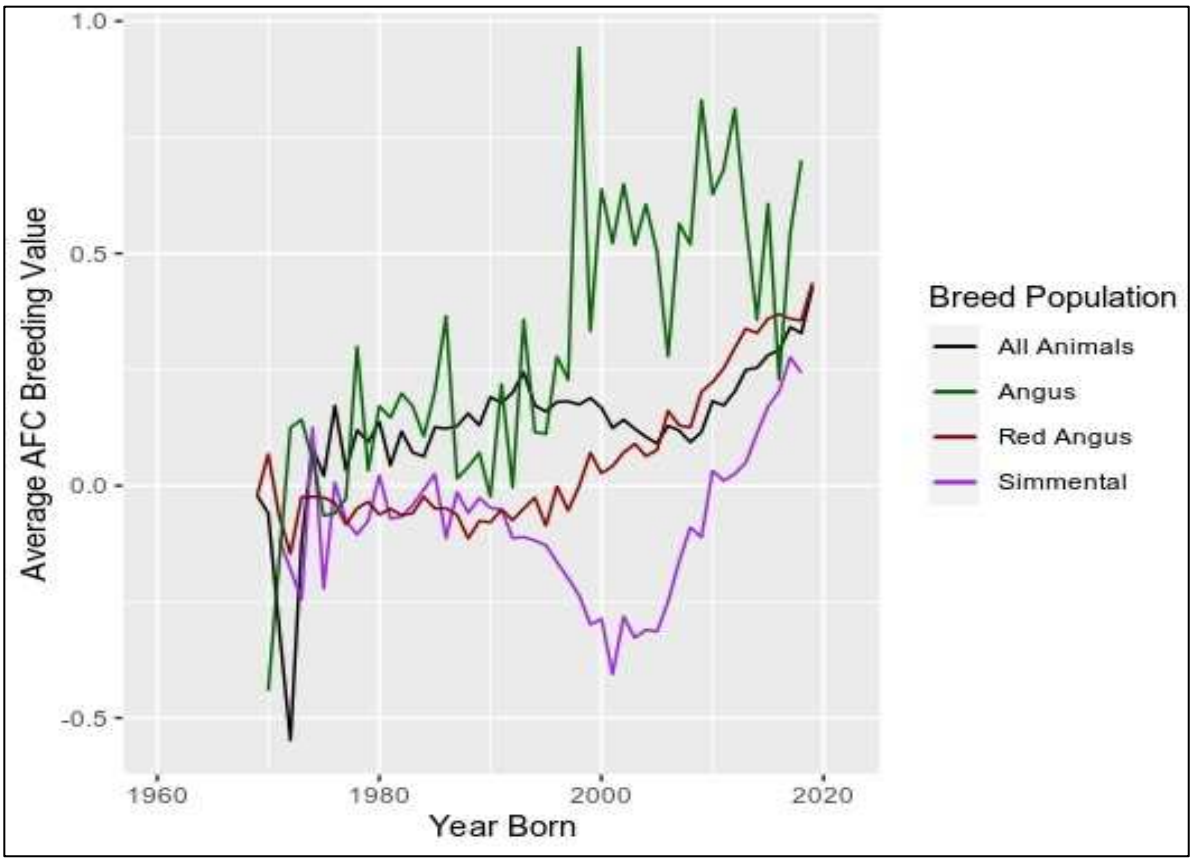

Figure 5.3. Genetic trend for age at first calving (AFC) by year of birth from a bivariate animal model including yearling weight (YW), when not accounting for age differences prior to first exposure.

5.4 Conclusion

This study investigated the genetic control of AFC in a multi-breed population of beef heifers to prototype the development of a genetic evaluation to select for animals that calve earlier in their lifetime and test the usefulness of AFC as a possible age covariate in subsequent heifer pregnancy evaluations. There is evidence of significant breed and heterosis differences relating to AFC. However, the most important factor influencing the expression of AFC is age differences before their first exposure. Many beef producers manage their heifers as a group and mass mate them all at the same time to reduce calving window variability. This practice artificially delays pregnancy and AFC in some animals, suggesting that variation in AFC may be due to managemental decisions rather than genetic merit. Older heifers in a CG

will not have the same opportunity to have a younger AFC compared to their younger counterparts. Fixing for these age differences better accounts for non-genetic influences causing variation, and helps ensure any potential genetic evaluation is appropriately attributing differences to genetics. This means that accounting for age differences in a CG is necessary for any AFC genetic evaluation. When accounting for DIFF, the majority of additive genetic variance was explained, and the heritability of AFC was near zero. This suggests that a raw difference in birth dates used in AFC phenotypes is a biased value and inappropriate for genetic evaluation or use as an age covariate in fertility genetic evaluations. This also suggests in beef production systems, advancing earlier calving is contingent upon enhanced management practices, as genetic selection will be insufficient to drive meaningful improvements.

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CHAPTER 6 - RANDOM REGRESSION MODELS FOR THE GENETIC EVALUATION OF HEIFER FERTILITY TRAITS IN A MULTI-BREED POPULATION OF BEEF HEIFERS

Summary

Traditional evaluations of heifer fertility traits generally use threshold animal models (TM) because pregnancy is a binary categorical outcome variable. Despite the successful implementation of TM for the evaluation of heifer pregnancy (HP), there are inherent challenges associated with the evaluation method. The first is the extreme category problem (ECP), when all observations in a contemporary group have the same outcome, resulting in poor or lack of convergence or removal of those data. The second is the lack of support in modern single-step genomic genetic evaluation software such as BOLT by Theta Solutions which implements the super-hybrid method for genetic evaluation. Because of data use issues in TM and the lack of support in some genetic evaluation software, random regression models (RRM) present an appealing alternative for evaluating binary or single-observation records like HP. The objectives of this study were then to investigate different methods for evaluating HP or related fertility traits in a multi-breed population of beef heifers. Data were retrieved from International Genetic Solutions (IGS) in February 2021. Data were in the form of binary exposure (1 = exposed; 0 = not exposed), binary pregnancy (1 = pregnant; 0 = not pregnant), and a breeding pasture contemporary group field. In addition, a full performance and pedigree file was retrieved to establish different age covariates and generate a 3-generation pedigree file. Two fertility traits evaluated using RRM were proposed; the first being the evaluation of heifer pregnancy by calving week (HPcw), which regresses a binary calving event on the week a heifer calved within her contemporary groups calving window, and the second being the linear evaluation of binary HP which regresses HP on an age covariate such as age at first exposure (AFE) or yearling age (YAGE). In all evaluation methods, Legendre polynomials were used as the base function and observed heritability estimates at different age ranges were transformed from the (co)variances estimated for the intercept and linear term of HPcw or HP. Within the HPcw evaluations, two separate

age covariates were proposed as additional fixed effects, with the first being age at first calving (AFC), and the second being AFE. Heritability estimates for HPcw fitting AFC as a fixed effect ranged from 0.39 to 0.56, though this is assuredly from AFC being a biased age estimate. Chapter 5 elaborated on the challenges associated with differences in heifer age prior to their first exposure. When accounting for these differences in heifer ages within contemporary group, the additive genetic variance explained in AFC is essentially 0. Observed heritability estimates for HPcw across 10 weeks, fitting AFE as a fixed effect ranged from 0.010 to 0.20, which are more realistic and consistent with literature estimates compared to observed HPcw heritability estimates fitting AFC as an age covariate. For the HP evaluation regressing HP on YAGE, heritability estimates ranged from 0.01 to 0.14, suggesting that up to 14% of the variation in HP across ages could be attributed to differences in additive genetics. For the evaluation regressing HP on AFE, heritability estimates were 0 or near zero, so this evaluation method likely requires additional scrutiny. Differences in heifer age covariate and trait definition for the evaluation of HP provided expanded opportunities for the development of national cattle evaluations using RRM. The potential advantages of utilizing RRM in evaluations of categorical or single observation data are that it allows the use of all available data in a dataset and is more adapted to single-step genomic evaluation software systems. Because of this, RRM may be the preferred evaluation method for HP or related fertility traits, though this requires additional testing in global databases.

6.1 Introduction

Heifer fertility traits are economically important for beef producers (Melton, 1995; Golden et al., 2000). However, fertility traits are lowly heritable and significantly influenced by a range of environmental and managemental factors (Cammack et al., 2009). Heifer pregnancy (HP) has been favored for many years as the primary trait in beef cattle genetic evaluation to help breeders make informed selection decisions for genetic improvement in heifer fertility. Breed associations, such as the American Angus Association, and the Red Angus Association of America, have implemented HP national cattle evaluations using a traditional approach adopting threshold animal models (TM) to evaluate the

binary trait. Genetic evaluations for HP differ from performance traits based on continuously observed traits because categorical traits such as HP violate many assumptions of normality (Henderson, 1975; Gianola, 1982), and as such a *maximum a posteriori* probit TM can be used to predict breeding values on the underlying scale (Gianola and Foulley, 1983; Harville and Mee, 1984; Falconer and Mackay, 1996).

While TM offer a solution by addressing the non-linear distribution of binary data, they can be impeded by the extreme category problem (ECP) when all animals in a contemporary group exhibit the same pregnancy outcome (no variation), leading to either convergence issues or unreliable estimates or the necessary data removal (Misztal et al., 1989). Removal of data from contemporary groups with no variation can distort inferences because the edited data would not be representative of the entire population (Misztal et al., 1989). Concurrently, TM have computational limitations, especially when integrating genomic data into large-scale genetic evaluations (Legarra et al., 2009). Notably, the more recent single-step genomic evaluation methods implemented using the hybrid and super-hybrid models in the BOLT evaluation software (Golden et al., 2018a) have not yet been adapted for TM (Fernando et al., 2014; Fernando et al., 2016). As a result, alternative models, such as random regression models (RRM), have gained attention due to their ability to account for non-linear data and adapt to longitudinal or single-observation traits in complex, multi-breed populations (Golden et al., 2018b). Examples of successful implementation of RRM for the evaluation of fertility traits can be seen in the evaluation of Stayability (Jamrozik et al., 2013; Golden et al., 2018b), though Speidel et al. (2018) provided the initial framework for adapting RRM for the evaluation of HP. While RRM were initially developed to evaluate longitudinal data, there have been instances where they were successfully adapted for single observation traits (Englishby et al., 2016; Speidel et al., 2018; Sanchez-Castro et al., 2020). Considering the challenges associated with TM for evaluating HP, RRM present an attractive alternative method for large-scale genetic evaluation of HP.

Though HP is observed as a categorical outcome, fertility is still age dependent as it relies on heifers reaching puberty, among other factors, though many beef production systems do not expose heifers at the onset of puberty and instead rely on fixed breeding windows. As such, evaluating HP using

RRM typically regresses the trait on an age covariate, such as age at first exposure (AFE; Sanchez-Castro, 2021), though there are other age covariate possibilities. This presents a unique opportunity for evaluating heifer fertility traits because there are financial incentives for having earlier calving heifers because they produce calves with heavier weaning weights, have a greater likelihood of subsequent breeding and have greater overall lifetime production (Wathes et al., 2014). For this reason, an alternative definition of HP based on the calving week (WK) of a heifer within a contemporary group using RRM was explored, as well as an attempt at replicating the same RRM approach presented by Speidel et al. (2018) and Sanchez-Castro et al. (2020). The objective of this study was then to investigate RRM for the evaluation of HP and related fertility traits in a multi-breed population of heifers.

6.2 Materials and Methods

Data used in this study were obtained from an existing database, and as such, an Institutional Animal Care and Use Committee (IACUC) approval was not required.

6.2.1 Data collection and description

Data were obtained from a historical database from the American Simmental Association (ASA) and International Genetic Solutions (IGS) genetic evaluation. The IGS genetic evaluation combines data from over 20 beef breed associations globally into a single multi-breed genetic evaluation. Heifer exposure and pregnancy data (n=740,423) were retrieved in February 2021 from IGS. There were 9 beef breed associations contributing heifer exposure and pregnancy data for this study (Table 4.1). Heifer exposure was the incidence of a heifer being exposed to a natural service sire or synchronized for artificial insemination. Heifer pregnancy was defined as the ability of a heifer to conceive and successfully remain pregnant until determined by ultrasound or successfully produce a calf and were binary observations (1 = Pregnant, 0 = Not Pregnant). However, breed associations involved in IGS are responsible for uploading records through a secure file transfer portal to the IGS database. Because of this, the criteria used by the breed associations to define exposure and pregnancy status may vary, similar to what was described in Chapter 3. While the definitions then may be related, inconsistencies across

organizations, while unknown, may potentially introduce errors that could affect the accuracy of genetic evaluations derived from this dataset. In addition, a performance data file including animal ID, breeder ID, herd ID, birth code, birth contemporary group, weaning management, weaning pasture, weaning contemporary group, yearling feed unit, yearling, contemporary group, serial birth date, serial weaning date, serial yearling date, birth weight, weaning weight, yearling weight, age of dam, sex, and calving ease code were retrieved on all animals and progeny in the study.

6.2.2 Heifer pregnancy by calving week

For the HP by calving week (HPcw) investigation, heifer pregnancy observations were defined by establishing a calving window and assigning success when a heifer produced a calf. A linear RRM using Legendre polynomials as the base function was used to regress HPcw on the week a heifer calved within a contemporary group and included a heifer age covariate in the model as a fixed effect. The start of the calving window was marked by the first calving event in each contemporary group, designating the beginning of week 1. Each subsequent week was defined as a seven-day period, with week 2 beginning 8 days after the initial calving, and so on, up to a maximum of 10 weeks (70 days). Heifers that calved within this 70-day period were assigned a binary outcome to indicate pregnancy success: a value of 1 was assigned if the heifer calved, while a 0 was assigned if the heifer did not calve within this period. For heifers that successfully calved, data were transformed so that they received a success observation (1 = success) for all weeks following their WK. For example, a heifer that calved in week 1 received a score of 1 for all 10 weeks, while a heifer that calved in week 3 received scores of 0 for weeks 1 and 2, followed by sequential 1's for weeks 3 to 10. Any heifer that failed to calve within the first 70 days was assigned a score of 0 for all weeks. Records from single-animal contemporary groups and CG with no variation in the 10^{th} week were removed from the study. Though this may eliminate groups with variation between different calving weeks, the cohort would consist of females that were all successful in pregnancy. As the primary purpose of this investigation was to try to identify an evaluation for HP, these animals were

removed. Further research could explore the inclusion of animals from contemporary groups with variation between weeks to better understand the relationship of calving week on fertility.

Two age covariates were initially considered for this study, with the first being age at first calving (AFC) and the second being age at first exposure (AFE). Age at first calving was defined as the difference in days between a heifer's serial birth date and her first calf's serial birth date. Records were limited to females calving between 630 and 810 days of age to remove extreme cases. The AFC threshold age range was the same used in Chapter 5. Females with embryo transfer or multiple birth progeny were removed from the study. Alternatively, AFE was also considered as an appropriate age covariate; however, in this dataset, breeding exposure windows were largely unknown. Thus, an assumption of gestation length was used to arrive at an approximate AFE. The estimate for AFE was determined by assuming the first heifer to calve in a contemporary group was the start of a calving window for a contemporary group, and the first day of exposure for a contemporary group could be arrived by subtracting 270 d from the serial birth date of the first calf. Therefore, AFE is the difference in days between a heifer's birth date and the assumed first day of exposure. As the data retrieved from IGS had some rare instances of integrity issues such as incorrect birth dates, extreme instances of AFE were noticed. In order to remove these instances, heifers with extreme AFE below 200 d and above 550 d were removed from the study. This included a similar age range reported by Sanchez-Castro (2021) but allowed for additional variation. This study was performed in parallel with the study described in Chapter 5, and a secondary investigation of this study was to determine if AFC could be used as a possible age covariate in an HP genetic evaluation to improve earlier calving. Comparing results from HPcw models fitting AFC or AFE allowed the ability to test this hypothesis.

6.2.3 Linear evaluation of heifer pregnancy

The linear RRM evaluation of HP was performed similarly to the methods presented by Speidel et al. (2018). This method involves regressing HP on an age covariate using RRM with Legendre polynomials. As discussed in Chapter 5, AFC may be an unsuitable age covariate as the difference in days

between when a heifer is born and when she produces her first calf depends on managerial decisions, such as when to first expose a group of heifers. For this reason, AFC was abandoned as a potential age covariate, and two other age covariates were considered instead. An estimate of a heifer's yearling age was the first age covariate considered. Yearling age (YAGE) was defined as the difference in days between a heifer's birth date and her age when a yearling weight observation was taken. Like before, AFE was the second age covariate used in the linear RRM methods for evaluating HP following the same procedure described above. Contemporary group (CG) was defined as a concatenation of breeder ID, herd ID, birth year, birth contemporary group, weaning contemporary group, and yearling contemporary group. Records from single-animal contemporary groups and CG with no variation were removed from the study.

Breeding exposure windows were generally known in the Red Angus population due to the requirements for data reporting by their breed association, and their existing genetic evaluation sets requirements on having a calf within 90 days after the onset of calving within a contemporary group. Despite these windows being reported to the RAAA, the data uploads to IGS did not support this field and thus were not known in the dataset used in this study. However, using the same assumption as used in establishing AFE, where the first calf born of a group of heifers is the start of a calving window, the difference in days between a heifer's calving date and the starting date within a contemporary group can be used to determine if a heifer calved within a particular calving window threshold. Two populations were selected, where if heifers calved after 90 days, a successful pregnancy outcome (1 = success) was changed to an unsuccessful outcome (0 = failure). Due to these populations exceeding many thousands of animals, and due to the complexity of some of the models, CG were filtered to narrow datasets to a more manageable number. This is not always ideal as the filtered dataset may not be entirely representative of the entire population. However, to ensure models were initiated and converged in an appropriate timeframe for variance component estimation, CG were further filtered to exclude animals from a CG with less than 5 animals, and CG with no variation were removed.

Fixed effects for both the HP and HPcw evaluations included CG and the appropriate age covariate (YAGE or AFE). Because findings from Chapter 4 indicated that breed differences and RHV were nominal in effect within same breed evaluations (though in some cases still statistically significant), these were not included as possible fixed effects in the HPcw and linear HP RRM models. Wald F-tests were performed simultaneously with variance component estimation using the statistical software package ASReml 3.0 (Gilmour et al., 2009) using equation 4.1.

6.2.4 Genetic evaluation of heifer pregnancy by calving week

A linear RRM using Legendre polynomials as the base function was used for the evaluation of HPcw. Depending on the model, either AFC or AFE were fit as a linear fixed effect age covariate, and HPcw was regressed on WK. The model in matrix form is presented in Equation 6.1 below:

$$y = Xb + Qu + Zpe + e \qquad \text{Eq. 6.1}$$

where ***y*** corresponded to a vector of binary HP observations, ***X*** was an incidence matrix relating observations in ***y*** to the contemporary group, the age covariate, and fixed regression coefficients for WK for the regression of HP on WK to their solutions in ***b.*** ***Q*** was an incidence matrix of WK covariates (representing the random regression effects of the WK on HP) relating WK observations in ***y*** to the random additive genetic regression coefficients in ***u.*** ***Z*** was an incidence matrix of WK covariates relating observations in ***y*** to permanent environmental random regression coefficients for each animal in ***pe***, and ***e*** was a vector of random residuals that included temporary environmental effects for each observation. Permanent environment was included in this method to account for non-genetic factors such as heifers being bred AI that led to a greater number of heifers calving in the first week compared to CG where heifers did not receive estrous synchronization and AI. The variances were then assumed to be:

$$var\begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & I \otimes P & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where ***A*** corresponded to Wright's numerator relationship matrix, ***G*** was the (co)variance matrix of the random additive genetic regression coefficients corresponding to the order of a linear Legendre

polynomial in the random regression; ***I*** was an identity matrix with an order equal to the total number of observations, ***P*** was the (co)variance matrix of the linear permanent environmental random regression coefficients corresponding to the number of calving weeks and σ_e^2 was the variance of random residuals.

6.2.5 Genetic evaluation of heifer pregnancy

Following the methods presented by Speidel et al. (2018), HP from the present study was regressed on AFE or YAGE, using a linear RRM with Legendre polynomials as the base function. The model equation in matrix form is presented in Equation 6.2 below:

$$y = Xb + Qu + e \quad \text{Eq. 6.2}$$

where ***y*** corresponded to a vector of binary observations of HP, ***X*** was an incidence matrix relating HP observations in ***y*** to unknown solutions for contemporary group and a linear fixed regression of HP on AFE in ***b***, Q was an incidence matrix consisting of the intercept and linear age covariates relating HP observations in ***y*** to the animal random additive genetic regression coefficients (intercept and linear slope) in ***u***, and ***e*** was the vector of unknown residual errors. The mean of the random effects was assumed to be 0, and variances were assumed to be:

$$Var\begin{bmatrix} Int \\ Lin \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_{int}^2 & 0 & 0 \\ 0 & A\sigma_{lin}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where ***A*** represents Wright's numerator relationship matrix, ***"Int"*** and ***"Lin"*** were the variances corresponding to the random additive genetic intercept and linear regression coefficients, respectively. The covariance between the intercept and the linear term was assumed to be zero since no heifers had more than one observation for HP (Speidel et al., 2018; Sanchez-Castro, 2021). ***I*** was an identity matrix with an order equal to the number of observations in ***y***, and σ_e^2 was the residual variance.

6.2.6 Statistical analysis

Data preparation was performed with the Animal Breeder's Tool Kit (ABTK; Golden et al., 1995) package of tools on the Colorado State University Center for Genetic Evaluation of Livestock (CGEL). A

3-generation pedigree file was developed for each population using the full pedigree obtained from IGS (~21 million animals). Table 6.1 provides a description of the HPcw and linear HP RRM models performed in this study.

Table 6.1. Description of random regression models performed for the evaluation of linear heifer pregnancy (HP), and heifer pregnancy by calving week (HPcw) in multiple breed populations.

Trait	Model #	Population	Fixed Effects	n of Records	n of Sires¥	n of Dams¥
HPcw	1	SIMUSA*	CG, AFC	24,088	7,455	40,591
	2	All BSHUSA	CG, AFC	1,924	2,134	5,377
	3	All RANUSA	CG, AFE	87,311	20,713	103,118
	4	All GBVUSA	CG, AFE	51,582	11,763	71,936
	5	SIMUSA€ CG >5	CG, AFE	44,527	14,245	77,317
	6	RANUSA€ CG>5	CG, AFE	18,430	9,539	40,099
HP on YAGE	7	RANUSA*	CG	18,156	5,325	27,815
	8	All SIMUSA	CG	82,064	17,172	102,994
HP on AFE	9	RANUSA€ CG>5	CG	9,207	6,589	24,483
	10	SIMUSA€ CG >5	CG	21,097	10,047	46,527

* Population was further subset by setting thresholds on CG size to reduce population size to a more manageable size. Otherwise, the models took multiple weeks to finish.
¥ Sire and dam counts are unique individuals represented in the 3-generation pedigree file.
€ Successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group.

All RRMs were performed using the leg(*v,n*) function. This function generates *n* + 1 Legendre polynomials, starting from order 0 (intercept), then 1 for linear and proceeding through higher-order terms up to *n*, based on the values in *v*. For example, to model a linear regression of HP on WK using the week (wk) predictor variable, the ASReml command would be leg(wk, 1). Detailed command files for modeling HPcw and HP can be found in Appendix B.

Variance components and heritability estimates from the evaluations of HPcw and HP were produced for the intercept and linear term by calculating the ratio of the additive to the phenotypic variances. However, variance components and heritability estimates obtained using RRM are not directly

comparable to those obtained through conventional models used in genetic evaluation (Speidel, 2011). This is because the estimates of (co)variance from RRM evaluations are in the form of additive direct, permanent environmental, and phenotypic variances for the shape of the polynomial. For both evaluation methods (HPcw and HP), a linear polynomial was implemented, and as such, the variances correspond to the intercept and linear term (slope) of the random polynomial. These variances can be transformed to calculate the observed variance estimate for HP and HPcw of the covariate used. For HPcw, this would be an observed heritability estimate for a specific WK, and for HP, this would be a heritability estimate for HP at a specific YAGE or AFE. This transformation is performed using the formula presented in Equation 6.3 below:

$$\widehat{\boldsymbol{G}} = \Phi \boldsymbol{K} \Phi' \qquad \text{Eq. 6.3}$$

where $\widehat{\boldsymbol{G}}$ represented the (co)variance matrix of HP observations at *t* given the regressed age covariate (WK, YAGE, or AFE). $\boldsymbol{K}$ was a matrix of order *k* that contained the RRM variance components for the intercept and linear term in the model. Φ was a matrix of order *t x k* (Mrode, 2014) containing the orthogonal polynomial coefficients evaluated at *t* standardized by the age covariate used with elements $\Phi_{ij} = \Phi_j(x_i)$ being the jth polynomial coefficient for the ith age covariate (Fischer et al., 2004; Speidel, 2011). An example of this transformation of converting (co)variances of the intercept and slope for HPcw into observed heritability by WK is described in Appendix C.

6.3 Results and Discussion

6.3.1 Heifer pregnancy by calving week

For the evaluation of HPcw, binary calving observations were regressed on calving week within a 70-d calving window in which a heifer produced a calf. A linear Legendre polynomial was used, and CG with no variation at week 10 were removed from the study. Cumulative calving rates for all heifers are presented in Figure 6.1, which illustrates that approximately 30% of heifers have usually had a calf within the first week of a calving window and gradually increase to 90% have calved by week 10. The cumulative calving rate reflects the total proportion of heifers that have calved up to each respective

week. The percentage of heifers that calve in the first week of a CG can vary widely based on several factors, including management, nutrition, and genetics, but perhaps the most substantial factor is the use of artificial insemination (AI; Perry and Cushman, 2013). Estrous synchronization significantly increases the likelihood of earlier calving (Lamb et al., 2006). Heifers bred to AI are typically timed to occur at the beginning of a breeding season (Minick-Bormann et al., 2006), such that heifers that successfully conceive at their first service will calve earlier and indicate the onset of a calving season for their CG mates. Moorey and Biase (2020) indicated that approximately 60% to 70% of heifers might calve in the first 3 weeks of a calving season, with a sequentially smaller proportion of the remaining pregnant heifers calving in successive weeks. Those estimates reported by Moorey and Biase (2020) are aligned well with the present study's multi-breed population, where approximately 60% of heifers have successfully calved in the first 3 weeks. Heifers that calve earlier in the calving season are often associated with improved reproductive performance and greater lifetime productivity (Lesmeister et al., 1973; Cushman et al., 2013). Earlier calving is also advantageous because heifers that calve earlier tend to produce heavier calves at weaning (Cushman et al., 2013).

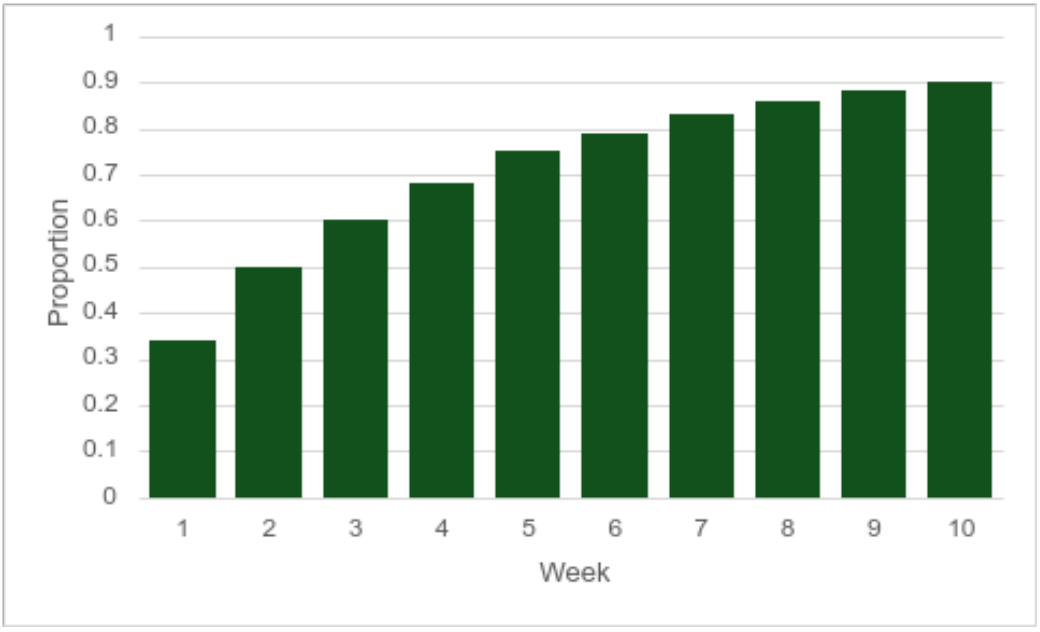

Figure 6.1. Cumulative calving rate by calving week in a multi-breed population of beef heifers.

In contrast, Figure 6.2 presents the weekly calving rate calculated from the pool of remaining pregnant heifers for all breeds of heifers, all SIMUSA heifers, all RANUSA heifers, and all BSHUSA heifers. This metric focuses specifically on the proportion of heifers that calved each week, considering only those that are pregnant and have not already calved. By isolating the weekly calving events, the calving dynamics over time are better understood. Because calving earlier in a calving season is economically relevant, the potential development of an HPcw using RRM can fundamentally change how producers select for improved heifer fertility while simultaneously improving earlier calving. Consistently across all breeds, the calving rate is highest in week 1, with calving rates near 30% for heifers in a CG, which is indicative of successful AI programs. Calving rates for Simmental and Shorthorn gradually decrease from around 25% to 15% as the calving window lengthens, whereas calving rates generally stay around 20% in Red Angus through week 10. The gradual diminishing in calving rates (weeks 2-10) could indicate the randomness of natural-service sires mating with heifers and varying estrous cycle lengths in heifers. On average, the estrous cycle is around 21 days but can range from 17 to 24 days due to differences in genetic or environmental factors (Lasley and Bogart, 1970; De Vries and Veerkamp, 2006).

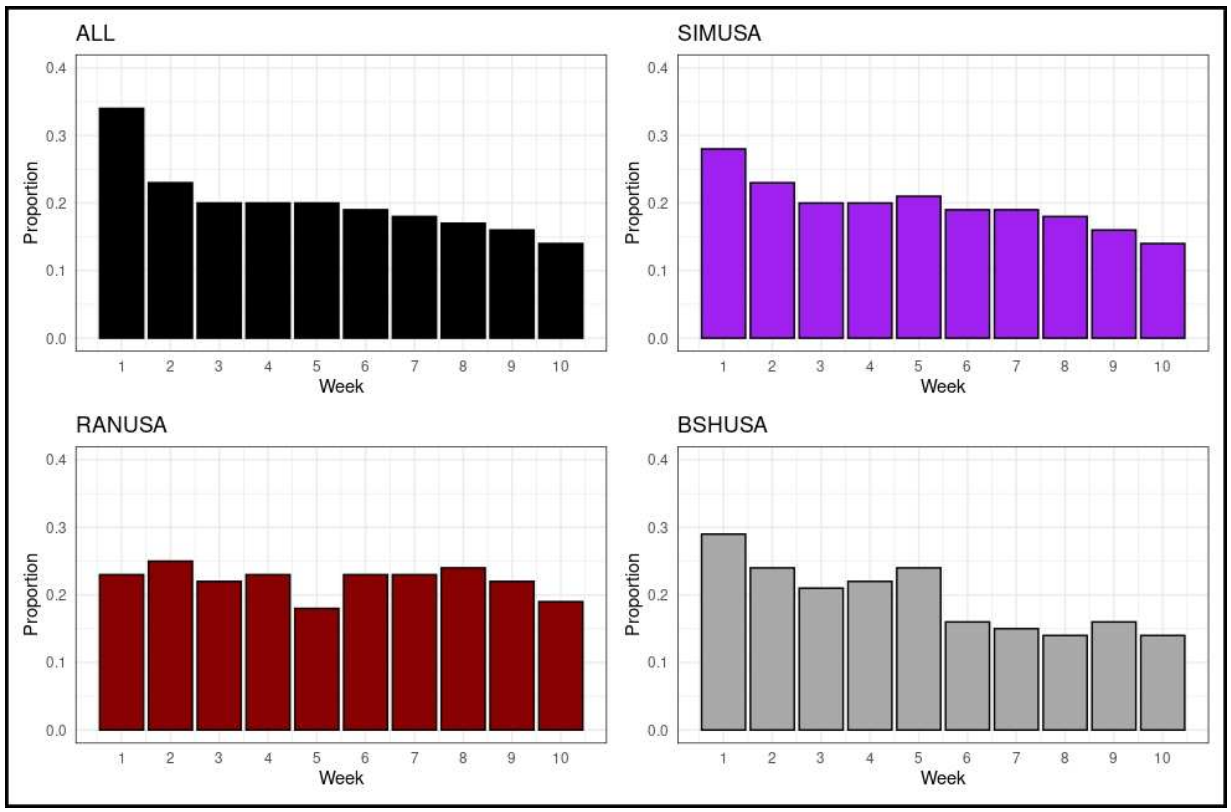

Figure 6.2. Weekly calving rates of pregnant heifers by week of calving event for all heifers (ALL), Simmental heifers (SIMUSA*), Red Angus heifers (RANUSA*), and Shorthorn heifers (BSHUSA*).

* Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022).

6.3.1.1 Using age at first calving as a fixed effect

For the evaluation of HPcw, HP was regressed on a given week within a calving window of 70-d and included either AFC or AFE as an additional age covariate fixed effect. Results from the HPcw evaluation using two separate breed populations and AFC as a fixed effect are presented in Table 6.2 and Table 6.3.

Table 6.2. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first calving (AFC) as a fixed effect in Simmental heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.063	0.047	0.072	0.182	0.395
2	0.063	0.034	0.060	0.157	0.382
3	0.063	0.023	0.051	0.137	0.371
4	0.063	0.015	0.044	0.122	0.361
5	0.063	0.009	0.040	0.112	0.356
6	0.063	0.005	0.038	0.106	0.358
7	0.063	0.004	0.039	0.106	0.368
8	0.063	0.005	0.042	0.111	0.383
9	0.063	0.009	0.048	0.120	0.403
10	0.063	0.015	0.057	0.135	0.423

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.

Model 1 used a subset population of Simmental heifers (SIMUSA), and model 2 used the full population of Shorthorn heifers (BSHUSA). The BSHUSA group was chosen for its relatively small animal count, high level of connectedness, and most importantly, the speed at which models converged. The SIMUSA population was further subset such that CG >= 50 and <= 100 heifers and appropriate variation in AFC was present. The justification for this was that there were 154,870 heifers with 10 observations for HPcw in the base population (n=1,548,700 total observations). A full SIMUSA population HPcw evaluation was attempted, and while iteration was occurring, the model failed to converge after 1 month and was abandoned. Before data filtering, there were 17,587 CG in the base SIMUSA population, and the minimum, mean, and maximum animal count for CG size were 1, 8.9, and 330, respectively. This meant additional CG filtering was required. There were 5,382 single animal CG, 17,028 CG with less than 50 animals, and only 126 CG with over 100 heifers. By filtering CG with >= 50 and <= 100 animals, there were 433 CG with 24,088 heifers.

Results from Table 6.2 indicate a curvilinear relationship between permanent environment (PE) and calving week, with higher PE variance in weeks 1-4 and near zero in weeks 5-9. There was a more minor curvilinear relationship between the additive variance and calving week. Phenotypic variance was

the sum of the residual, PE, and additive variances for a given week, and the ratio of the weekly additive variance over the weekly phenotypic variance was the heritability estimate. The minimum, average, and maximum heritability estimates for HPcw in SIMUSA heifers were 0.356, 0.380, and 0.423, respectively.

Table 6.3. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first calving (AFC) as a fixed effect in Shorthorn heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.047	0.083	0.081	0.210	0.386
2	0.047	0.058	0.075	0.180	0.416
3	0.047	0.039	0.070	0.155	0.450
4	0.047	0.023	0.066	0.135	0.485
5	0.047	0.012	0.063	0.121	0.519
6	0.047	0.005	0.061	0.113	0.544
7	0.047	0.002	0.061	0.110	0.556
8	0.047	0.004	0.062	0.113	0.552
9	0.047	0.010	0.064	0.121	0.533
10	0.047	0.020	0.068	0.134	0.504

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.

Results in Table 6.3 were similar to those presented in Table 6.2. However, there was a more extreme curvilinear relationship between PE and WK and a relatively flat relationship of additive variance across WK. Because of this, heritability for HPcw started lower in weeks 1-3 and increased before leveling in weeks 4-9, with a slight drop in heritability in week 10. The minimum, average, and maximum heritability estimates for HPcw in BSHUSA heifers were 0.386, 0.495, and 0.556, respectively. There was less residual variance in the BSHUSA group compared to the SIMUSA group. The additive variance in the BSHUSA group was higher across all weeks than the SIMUSA group, leading to higher overall heritability. Despite these small differences, the overall shape of the heritability trends for HPcw using AFC as an age fixed effect across WK between BSHUSA and SIMUSA were similar. However, most evaluations of calving date, first-service conception, or age at first calving produce heritability estimates

that are typically low to moderately heritable (<0.10 to <=0.30; Cammack et al., 2009), suggesting these heritability estimates are likely overestimated.

A possible cause is that sequential 1's were used to indicate calving success, such that when a heifer had successfully produced a calf through a given week, she would have a successful observation. If a heifer calved in week 1, she would have a series of successful observations through week 10. However, it would be impossible for a heifer to have calved every week. This method of sequential 1's could introduce redundant data points, as it implies that a heifer could calve multiple times within the same season, which is biologically impossible. Repeated, identical observations may create artificial correlations that the evaluation interprets as genuine patterns (Silk et al., 2020), and the model might misattribute variation due to repeated measurements as true underlying variability. In response to this, an attempt was made to transform these datasets such that after the initial success observation, each successive 1 was modified to be a missing value (" . "). Despite this transformation, models failed to converge, and results were not estimable. This could be due to the data structure being imbalanced for each week and across contemporary groups, or the model struggling to reach converge due to how it evaluates missing values. However, the reasons for this non-convergence are unclear and warrant further investigation.

A second possible explanation is that during the model development process, Models 1 and 2 were performed parallel to the AFC evaluations presented in Chapter 5. Literature estimates almost wholly ignore the influence of varying ages of heifers in a CG before their first exposure (Frazier et al., 1999; Gutierrez et al., 2002; Bormann et al., 2010; Berry et al., 2014; Brzakova et al., 2020; Pardo et al., 2020; Gonzalez-Murray et al., 2021). This would not be an issue if heifers were first exposed once they have reached puberty; however, most beef production systems in North America wait until a fixed date to mass mate an entire group of heifers (Bullock, 2014). The reason for this is that beef producers prefer to mate heifers when an appropriate body condition has been reached rather than as early as possible and regulating the length of the breeding season facilitates better management and resource allocation during shorter calving periods (Byerly et al., 1987; Funston et al., 2004). Because of this factor, Smith et al.

(1989) acknowledged that when accounting for heifer day of birth in an AFC prediction model, the birthdate can almost wholly explain AFC. Martinez-Velazquez et al. (2003) accounted for the month of birth and age at puberty in an AFC model and reported a direct heritability of 0.08 ± 0.04. Results from Chapter 5 indicate that not accounting for age differences before a heifer's first exposure significantly inflates the additive variance of AFC. The inflated variance component results obtained from the present study of modelling HPcw with AFC as an age covariate were what led to much of the investigation into AFC described in Chapter 5. In response, the second proposed age covariate was AFE and results from HPcw evaluations using AFE as a fixed effect are discussed.

6.3.1.2 Using age at first exposure as a fixed effect

The evaluation of HPcw was further tested by integrating AFE as a fixed effect in the evaluation, because calving week does not account for animal age prior to exposure. Records for AFE were limited to a minimum of 200 d and a maximum of 550 d. Heifers with an AFE outside this range were modified to have missing values (" . "). Though establishing AFE required an assumption on gestation length, the summary statistics for AFE (Table 6.4) were remarkedly similar to those presented by Sanchez-Castro (2021). The Gelbvieh population (GBVUSA) had the lowest average AFE (401.8), and the modified SIMUSA population had the highest (422.0). These estimates are consistent with the current practices of most beef production systems, where producers will breed heifers approximately 1-2 months after the end of their usual calving season. Heifers born earlier in a group will have an older AFE than their younger CG mates. There were several instances where there were extreme AFE estimates on the low side (<100) and even negative. This is likely due to errors in data reporting that potentially indicate heifers are of the same CG but born in different years. These extreme instances were removed from subsequent evaluations.

Table 6.4. Summary statistics for the age at first exposure (AFE) covariate used in 4 different evaluations of heifer pregnancy by calving week (HPcw).

Model	Breed	n	Min	Mean	Max	Var	SD
3	RANUSA	84,266	200	419.4	530	1,346.9	36.7
4	GBVUSA	49,150	200	401.8	526	2,430.3	49.3
5	SIMUSA€ CG >5	44,527	200	422.0	532	1,029.1	32.1
6	RANUSA€ CG>5	18,430	200	419.5	518	963.0	31.0

€ Successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group.

The age data from AFE were included as a fixed effect to better account for the ages of heifers as they entered a breeding season. Since heifers would have repeated records for calving success, a block of equations for PE was included, but this could be argued as unnecessary. As described before, these repeated and identical records may inappropriately create artificial correlations between calving weeks. While it can be argued that accounting for PE in these equations is unnecessary, adding a block of equations for PE can help account for differences in management, such as the use of AI, that could introduce additional variation in reproductive performance across calving week. For instance, some heifers first exposed through AI may have different conception/pregnancy dynamics when compared to those only exposed to natural-service sires. By modeling PE in these evaluations, the aim is to capture the effects of these differing non-random management practices. The following tables provide the variance components for the evaluation of HPcw for each of the 4 different populations. Table 6.5 provides the observed weekly variance component estimates from Model 3 in a population of Red Angus heifers.

Table 6.5. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first exposure (AFE) as a fixed effect in Red Angus heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.054	0.161	0.024	0.239	0.100
2	0.054	0.130	0.017	0.202	0.085
3	0.054	0.104	0.012	0.170	0.068
4	0.054	0.083	0.007	0.144	0.050
5	0.054	0.066	0.004	0.124	0.032
6	0.054	0.053	0.002	0.109	0.018
7	0.054	0.044	0.001	0.100	0.011
8	0.054	0.041	0.001	0.096	0.015
9	0.054	0.041	0.003	0.098	0.030
10	0.054	0.046	0.006	0.106	0.054

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.

Results from Table 6.5 indicate the relationship between PE and WK was higher in weeks 1-3 before decreasing to near 0 in weeks 6-10. This same parabolic trend held true with additive variance as well, where the additive variance in weeks 1-3 was notably higher before decreasing and nearing 0 in weeks 5-10. This resulted in heritability estimates that were higher in weeks 1-3 than estimates in later weeks. The higher observed heritability estimates in the earlier weeks of HPcw could be advantageous for selection of pregnancy for earlier calving. They indicate that a greater proportion of the genetic variation is observed in the earlier weeks, and a genetic evaluation that couples selection pressure of pregnancy with earlier calving could be possible. The minimum, average, and maximum heritability estimates for HPcw in this evaluation of RANUSA heifers were 0.011, 0.047, and 0.100, respectively. This curvilinear trend in heritability estimates suggests there may be varying genetic influence on HP over time, as the observed PE effect is also curvilinear. The decrease in observed heritability in the middle weeks could due to potential randomness in conception occurring in breeding pastures.

Table 6.6. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first exposure (AFE) as a fixed effect in Gelbvieh heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.058	0.100	0.035	0.193	0.181
2	0.058	0.081	0.024	0.163	0.149
3	0.058	0.064	0.016	0.138	0.114
4	0.058	0.050	0.009	0.117	0.081
5	0.058	0.038	0.005	0.101	0.054
6	0.058	0.029	0.004	0.091	0.041
7	0.058	0.023	0.004	0.085	0.050
8	0.058	0.019	0.007	0.084	0.083
9	0.058	0.018	0.012	0.087	0.136
10	0.058	0.019	0.019	0.096	0.199

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.

Model 4 used a population of Gelbvieh heifers, and the results are presented in Table 6.6. There was a similar curvilinear relationship between PE and WK. The additive variance was lowest from weeks 4-8 but increased on the tail ends of WK. This resulted in a more typical parabolic curve in heritability estimates across WK. The minimum, average, and maximum heritability estimates for HPcw in this evaluation of GBVUSA heifers were 0.047, 0.109, and 0.199, respectively. The heritability estimate in week 10 was the highest, opposite from the previous model using Red Angus heifers. In general, the heritability for HPcw across weeks was higher in this Gelbvieh population than in the Red Angus population.

Table 6.7. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first exposure (AFE) as a fixed effect in a modified population of Simmental € heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.061	0.146	0.019	0.227	0.085
2	0.061	0.125	0.013	0.199	0.066
3	0.061	0.107	0.008	0.176	0.046
4	0.061	0.093	0.005	0.159	0.029
5	0.061	0.084	0.002	0.147	0.016
6	0.061	0.078	0.001	0.140	0.010
7	0.061	0.076	0.002	0.139	0.014
8	0.061	0.078	0.004	0.143	0.025
9	0.061	0.084	0.007	0.152	0.044
10	0.061	0.094	0.011	0.166	0.067

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.
€ Successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group. CG was filtered such that animals in groups with <=5 heifers were removed.

Model 5 used a population of Simmental heifers with a differing CG strategy, where successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group. CG was filtered such that animals in groups with <=5 heifers were removed. Regardless, similar trends for HPcw are present from the results in Table 6.7 compared to the two previous evaluations. The residual variance is higher in this group compared to the GBVUSA and RANUSA populations. There is a less pronounced curvilinear relationship between PE and WK in this population compared to the two previous RANUSA and GBVUSA evaluations. However, the PE variance estimates are considerably higher than the previous evaluations, which suggests there may be more consistent non-genetic factors contributing to the variation in calving success across all weeks. This could result from how HP phenotypes were established from whole herd reporting (WHR) information (discussed in Chapter 3) rather than directly reported from producers. In general, there were lower heritability estimates across all weeks compared to the previous breed evaluations. However, this is consistent with heritability estimates obtained using TM methodology for Simmental

heifers compared to Red Angus and Gelbvieh heifers (results from Chapter 4), where SIMUSA had lower estimates of heritability in HP compared to both other breeds. The minimum, average, and maximum heritability estimates for HPcw in this evaluation of SIMUSA heifers were 0.010, 0.040, and 0.085, respectively. Due to the pronounced parabolic trend observed in the additive genetic variance, heritability estimates exhibited a more distinguished curvilinear pattern, with notably higher values at the extremes of the WK distribution than the midpoints.

A potential reason for this inflation is an inherent function of using Legendre polynomials, and although they help reduce the correlation between successive observations, they tend to place higher emphasis on observations on the extreme ends of an age data range (Kirkpatrick et al., 1990; Meyer, 2005). As a result, RRM using Legendre polynomials as the base function tends to inflate variances at the extremes of an age data range (Yin et al., 2012). This occurs because RRM are sensitive to changes in data distribution, particularly to reductions in the number of records associated with the age covariate implemented (Brugemann et al., 2013). In the case of this evaluation method, where only 70-d separates the distribution, there is still a noticeable pattern of more extreme inflation of variances at the tail ends of the WK range. However, since all heifers have an observation for every WK, perhaps this inflation is instead due to double counting of successful observations in successive weeks after the initial calving event.

Table 6.8. Observed weekly (Weeks 1-10*) variance components for heifer pregnancy by calving week (HPcw) using age at first exposure (AFE) as a fixed effect in a modified population of Red Angus € heifers.

Week	σ_e^2	σ_{pe}^2	σ_a^2	σ_p^2	h^2
1	0.058	0.160	0.018	0.236	0.074
2	0.058	0.137	0.013	0.207	0.061
3	0.058	0.118	0.009	0.184	0.046
4	0.058	0.104	0.005	0.167	0.032
5	0.058	0.094	0.003	0.155	0.020
6	0.058	0.089	0.002	0.149	0.012
7	0.058	0.089	0.001	0.148	0.009
8	0.058	0.093	0.002	0.153	0.012
9	0.058	0.102	0.003	0.163	0.020
10	0.058	0.116	0.006	0.179	0.032

* Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.
€ Successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group. CG was filtered such that animals in groups with <=5 heifers were removed.

Finally, Model 6 used a population of Red Angus heifers, with a differing CG filtering strategy compared to Model 3, where successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group. CG was filtered such that animals in groups with <=5 heifers were removed. Like the previous evaluations, similar trends in PE variance, additive variance, and heritability were observed in Table 6.8. Through additional removal of animal records, there were slight changes in the variance components estimated from Model 6 compared to Model 3. The residual variance was slightly higher (0.058 versus 0.054), the PE variance across weeks was of a similar shape, though with higher estimates across all but week 1, and the resulting heritability estimates were notably lower across all weeks in comparison. The minimum, average, and maximum heritability estimates for HPcw in this evaluation of RANUSA heifers were 0.011, 0.047, and 0.100, respectively. Figure 6.3 provides all the transformed observed estimates of HPcw heritability for each WK across the 4 models (Models 3-6) featuring different breed populations.

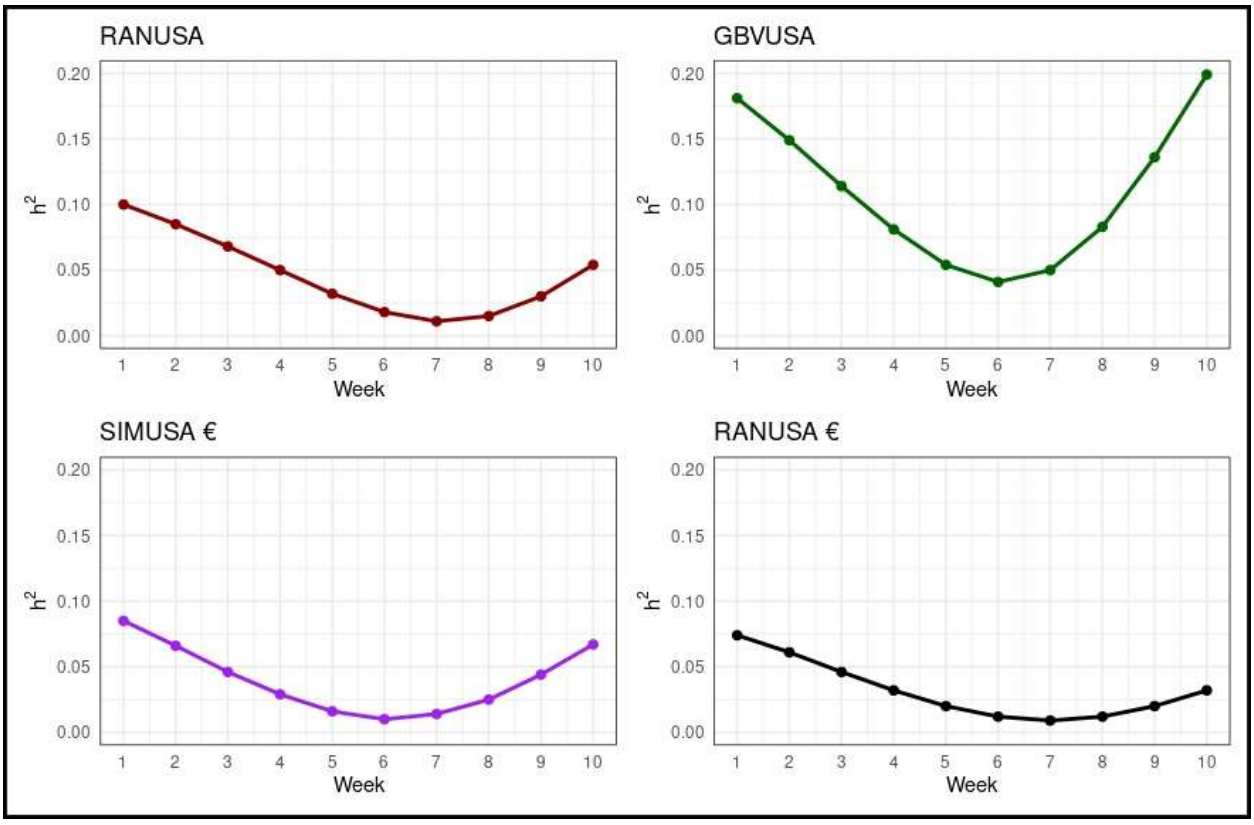

Figure 6.3. Observed heritability estimates of heifer pregnancy by calving week (HPcw) for each calving week (WK) in Red Angus (RANUSA), Gelbvieh (GBVUSA), a modified Simmental population (SIMUSA €), and a modified Red Angus population (RANUSA €) of heifers, while fitting age at first exposure (AFE) as a fixed effect.

* Follows the standard methods for animal identities defined by the International Committee for Animal Recording (ICAR), where the first 3 characters are a breed code, and the following 3 characters are a country code (ICAR, 2022).
** Variances obtained for the intercept and slope were converted to an observed weekly estimate using a transformation process.
€ Successful observations for HP were modified to failures (0 = Not pregnant) if heifers calved after 90 d from the beginning of the calving season in a contemporary group. CG was filtered such that animals in groups with <=5 heifers were removed.

It appears that heritability is higher in the earlier weeks, even when considering potential Legendre polynomial inflation. These data show that the additive genetic variance and heritability trends for HPcw across 10 weeks are similar across different breeds of cattle, suggesting there is similar genetic control of HPcw regardless of breed. Despite similar trends in the early weeks, Model 4, featuring GBVUSA heifers, contrasts slightly as the heritability estimates decline until week 6 and then increase

sharply, peaking in week 10. This pronounced change in GBVUSA highlights substantial genetic influence in the later weeks of the calving period compared to the other breeds studied. This may be because of increased breed-specific genetic control due to the population having lower PE variance and higher additive genetic variance in the later weeks. The pattern of higher heritability estimates in earlier weeks suggest that genetic contributions to HPcw are more significant in the earlier calving weeks, and selection for improved HPcw would be more responsive by focusing on the earlier weeks. This is likely due to the heifers that calve earlier in the calving window were successful despite fewer opportunities to become pregnant. This means that selecting for heifers that calve earlier in the calving season could yield more genetically consistent outcomes as opposed to selecting for mid-season calving. This could provide a fundamentally innovative opportunity for tandem improvement in heifer reproductive fitness as well as earlier calving, which are both economically relevant traits.

The HPcw in week 1 is a similar, if not the same, trait as first service conception rate (FSCR) when assuming all heifers were exposed via AI in a CG (Sanchez-Castro et al., 2020). Though the comparison is not exact, heritability estimates from the present study for HPcw in week 1 are within the heritability estimates (0.02-0.12) from focal age ranges (360-430d for age at first insemination) in Angus heifers presented by Sanchez-Castro et al. (2020), however the authors also admit that heritability estimates on the extremes of an age distribution are likely inflated due to meaningful reductions in the number of records associated with a particular age. However, in this multi-breed population, it is unknown and likely inappropriate to assume that all heifers were first exposed to AI. Despite this it may be a reasonable assumption that when particular CG of heifers were first exposed via AI, that all heifers within that CG were first exposed via AI. Though, a female that became pregnant and produced a calf from her first AI would be theoretically equivalent to a naturally bred heifer that successfully became pregnant and produced a calf within 21 d of the breeding season (Cammack et al., 2009). Combining both FSCR AI records and calving success within 21 d of a calving window was proposed by Donoghue et al. (2004a,b), and when treating these as the same trait the authors reported a heritability estimate for this "combined" evaluation of 0.036± 0.007. Their results indicated that heifers with a higher probability to

conceive first-service mated using AI, also have a higher probability of conceiving when mated via natural service (Donoghue et al., 2004a). With the exception of GBVUSA, their results are similar with the heritability estimates obtained from the present study at week 3 of HPcw (0.046-0.68 excluding GBVUSA), which would be a similar trait definition. In general, FSCR is reported as a lowly heritable trait ranging from 0.03 to 0.22 (Dearborn et al., 1973; Minick-Bormann et al., 2006; Cammack et al., 2009).

Conception per estrous cycle was another related fertility trait proposed by Dearborn et al., (1973), that evaluated the reproductive performance of subsequent estrous cycles for cows that failed to conceive on first service. They used a marking harness on natural service sires to record a mating event in cows and used a 3-week interval to distinguish between estrous cycles, up to 4 cycles (~84 d). Using this method, the authors reported a heritability estimate of 0.27 ± 0.17, however this method of phenotype collection is intensive and likely too cumbersome for practical application. Their estimate of heritability is higher than any heritability estimate observed at week 10 in any of the models performed in the present study, though if calving week were extended an additional 2 weeks the trends observed would suggest observed heritability would increase at week 12. Dearborn et al. (1973) evaluated the cumulative conceptions per estrous cycle which was approximately 84 d in length, whereas MacNeil et al. (1984) evaluated individual conceptions per service, however they reported a markedly lower heritability estimate of 0.03 for the trait. Considering calving in WK 1 would be the same as conceiving first service AI, or the earliest mating occurring in a breeding pasture with a natural service sire, the estimate from MacNeil et al. (1984) is consistent estimates for WK 1 in the present study. However, due to randomness of mating in subsequent weeks it is difficult to compare heritability estimates from WK 2-10 to the evaluation proposed by MacNeil et al. (1984).

The heritability estimates across different calving weeks suggest there is a variable genetic influence on heifer pregnancy depending on the timing within the calving season. However, developing HPcw as a trait for national cattle evaluation still presents some interesting challenges, such as the expression of the trait. It is possible to model the trait as a series of weekly success events and reflect the

probability of a heifer being pregnant by a calving week. Estimated breeding values (EBV) produced from this series of weeks could be converted into a composite value or index that combines the weekly breeding values for successive weeks. This could be done by weighting the weekly EBV according to their economic importance. Considering that producers have two economic goals of 1) improving fertility rates in heifers, and 2) ensuring heifers calve early in a calving season, this RRM approach for HPcw has appeal because you could theoretically weight WK 1-3 higher than the mid-weeks in a selection index. You could then appropriately weight the probability of having a calf by at least week 10 to ensure fertility is achieved. The other possibility is to choose a week as the trait of interest (e.g. WK 1 or WK 10) and estimate breeding values for that specific week. The potential drawback of this is that this no longer becomes a traditional HP genetic evaluation, but rather a probability of calving by a given week genetic evaluation. Regardless of approach, there are still some concerns as to modelling successive 1's in this model, and the inflation of variances at the extremes of the WK range must be considered.

6.3.2 Linear evaluation of heifer pregnancy

Though RRM are designed to evaluate longitudinal data and repeated records over time, there are examples of their successful implementation into single observation traits and most notably in fertility traits with the methods presented by Speidel et al. (2018) and Sanchez-Castro et al. (2020). Following the initial framework presented by Speidel et al. (2018), this study used RRM to predict HP in Red Angus and Simmental heifers. Since HP was a binary observation, observed once in a heifer's life, the model equation does not include a block of equations for PE and does not contain a non-zero additive genetic covariance between the intercept and linear components of the random regression coefficients. Two potential age covariates were considered and tested, the first being YAGE and the second being AFE. The observed YAGE is the difference between when a heifer is born and when she has a yearling weight observed and tends to be a reliable indicator of age before entering a breeding pasture, as many production systems will typically initially expose entire groups of heifers via AI or released to a breeding pasture approximately 1-2 months after YAGE are observed. Since the difference in days between when

YAGE is observed in groups of heifers and the onset of their first exposure is a constant value. Therefore, YAGE can be a reliable estimate of developmental progress before exposure to breeding. The second age covariate considered was AFE, which relies on an assumption of gestation length (270 d) to be established because breeding exposure dates are unknown in this dataset. Both age covariates were tested in the subsequent analysis, where binary HP was regressed on either YAGE or AFE using random regression models.

6.3.2.1 Using yearling age as regressed age data

Summary statistics for YAGE used in Models 7 and 8 are presented in Table 6.9. The evaluation featuring RANUSA was further subset such that CG >= 50 and <= 100 heifers were removed to ensure timely iteration of variance components. All heifers in the RANUSA population observed YAGE, but this was not the case in the SIMUSA population. Heifers that did not have an observed YAGE had their HP records still included but with missing values for the age covariate. The Beef Improvement Federation (BIF) recommends taking yearling weight measurements between 320 and 410 days of age, and these data are typically standardized by adjusting for age of dam and calf age at weighing for genetic evaluations (BIF, 2021). However, using YAGE as an age covariate also allows for the assessment of heifer maturity before breeding and aligns well with the importance of heifer development and timing in reproductive success (Martin et al., 1992; Funston and Deutscher, 2004). Data from Table 6.9 suggests that, on average, heifers in both populations are at or around 1 year of age when their yearling weight is recorded. The relatively low standard deviations indicate only moderate variability in age. This results in a relatively uniform age distribution in both populations.

Table 6.9. Summary statistics for the yearling age (YAGE) covariate used in 2 separate evaluations of heifer pregnancy (HP) using random regression models.

Model	Breed	n	Min	Mean	Max	Var	SD
7	RANUSA*	18,156	270	362.1	500	1,333.3	36.5
8	SIMUSA	26,141	270	365.9	499	1,601.5	40.0

* The Population was further subset by setting thresholds on CG size to reduce it to a more manageable size. Otherwise, the models took multiple weeks to finish.

Results of variance component estimation from Model 7 are presented in Table 6.10. Heritability was calculated as the ratio of weekly additive genetic variance (σ_a^2) over the weekly phenotypic variance (σ_p^2), with the weekly phenotypic variance being the sum of the residual (σ_e^2) and additive variances for each respective week. In this population of Red Angus heifers, the observed heritability estimate at 375 d was 0.016, which is lower than the estimates obtained from linear animal models (LM) and threshold animal models (TM) for the same breed in results presented in Chapter 4. However, the estimate is closer to the heritability obtained using LM methods. The minimum, mean, and max heritability estimate in this population of Red Angus heifers was 0.016, 0.067, and 0.14, respectively. This suggests that up to 14% of the variation within HP were attributable to differences in additive genetics. These estimates are similar with those presented in literature (Mathiews et al., 1995; Evans et al., 1999; Cammack et al., 2009; Boldt et al., 2018; Sanchez-Castro, 2021).

Table 6.10. Observed variance components for heifer pregnancy (HP) regressed on yearling age (YAGE) using random regression models in a subset population of Red Angus heifers.

YAGE	σ_e^2	σ_a^2	σ_p^2	h^2
270	0.159	0.026	0.184	0.140
291	0.159	0.018	0.177	0.102
312	0.159	0.012	0.170	0.069
333	0.159	0.007	0.166	0.043
354	0.159	0.004	0.163	0.025
375	0.159	0.003	0.161	0.016
396	0.159	0.003	0.161	0.017
417	0.159	0.004	0.163	0.026
438	0.159	0.008	0.166	0.045
459	0.159	0.012	0.171	0.072
480	0.159	0.019	0.177	0.105
499	0.159	0.026	0.184	0.140

* Population was further subset by setting thresholds on CG size to reduce population size to a more manageable one. Otherwise, the models took multiple weeks to finish.

Results of variance component estimation from Model 8 are presented in Table 6.11. In this population of Simmental heifers, the observed heritability estimate at 375 d was 0.009, which is lower than the observed heritability estimates for the same age in the previous evaluation, and lower than estimates obtained in Simmental heifers using LM and TM methodology (Chapter 4). However, a similar trend of observed heritability across the distribution of YAGE is observed in this population (Figure 6.4) as the previous evaluation, as well as the trends presented by Sanchez-Castro (2021). The minimum, mean, and max heritability estimates in this population of Red Angus heifers were 0.009, 0.056, and 0.12, respectively. This still suggests that up to 12% of the variation within HP is attributable to differences in genetics and consistent with literature estimates (Mathiews et al., 1995; Evans et al., 1999; Cammack et al., 2009; Boldt et al., 2018; Sanchez-Castro, 2021).

Table 6.11. Observed variance components for heifer pregnancy (HP) regressed on yearling age (YAGE) using random regression models in Simmental heifers.

YAGE	σ_e^2	σ_a^2	σ_p^2	h^2
270	0.114	0.016	0.130	0.124
291	0.114	0.011	0.125	0.088
312	0.114	0.007	0.121	0.058
333	0.114	0.004	0.118	0.034
354	0.114	0.002	0.116	0.018
375	0.114	0.001	0.115	0.009
396	0.114	0.001	0.115	0.010
417	0.114	0.002	0.116	0.019
438	0.114	0.004	0.118	0.036
459	0.114	0.007	0.122	0.061
480	0.114	0.012	0.126	0.092
499	0.114	0.016	0.130	0.124

* Population was further subset by setting thresholds on CG size to reduce population size to a more manageable one. Otherwise, the models took multiple weeks to finish.

Though the residual variance was lower in Model 8 compared to Model 7, this was generally the case when using LM or TM methodology, where the additive variance in HP estimated in Simmental heifers was generally lower compared to the additive variance of HP estimated in Red Angus heifers. It's worth acknowledging, however, that a potential reason for the lower additive variance observed in the Simmental group could also be attributed to the inclusion of HP records without a YAGE observation. In both evaluations, the general trend was that the additive variance decreases from its youngest age (270 d) to near 0 at around 375 d before gradually increasing at the oldest age (499 d). This trend suggests that the genetic influence on HP is highest at the extremes of the YAGE range, with reduced genetic variability during the middle ages. This same trend is observed in the heritability estimates, suggesting that the genetic contribution of HP success is more pronounced at younger or older ages when yearling weights are observed. In practice, this could suggest that heifers who are older when yearling weights are observed who fail to conceive likely have a genetic predisposition for reduced fertility because they have had ample opportunity to receive developmental resources and have reached sexual maturity. Interchangeably, this also suggests that heifers who are younger when yearling weights are observed and

successfully conceive and remain pregnant likely have a genetic predisposition for improved fertility despite a disadvantaged opportunity for development to sexual maturity. Byerley et al. (1987) reported differences in pregnancy rates in heifers first exposed at the onset of puberty versus heifers first exposed at their 3rd estrus. The implications of this suggest that younger heifers have had fewer estrous cycles, and though fertility rates increase with increasing age, younger heifers who successfully conceive are more economically desirable for their improved fertility and earlier calving. However, as was previously mentioned, an inherent challenge with the use of Legendre polynomials is the inflation of variances at extreme edges of age ranges or in ages with little phenotype representation. Considering this inflation, it can be assumed that the heritability estimates observed from both models at more extreme YAGE ranges are likely inflated and are higher than should be expected. Similar to what was observed by Sanchez-Castro (2021), the parabolic shape of the observed heritability for HP on YAGE is seen in the present study's results in Figure 6.4.

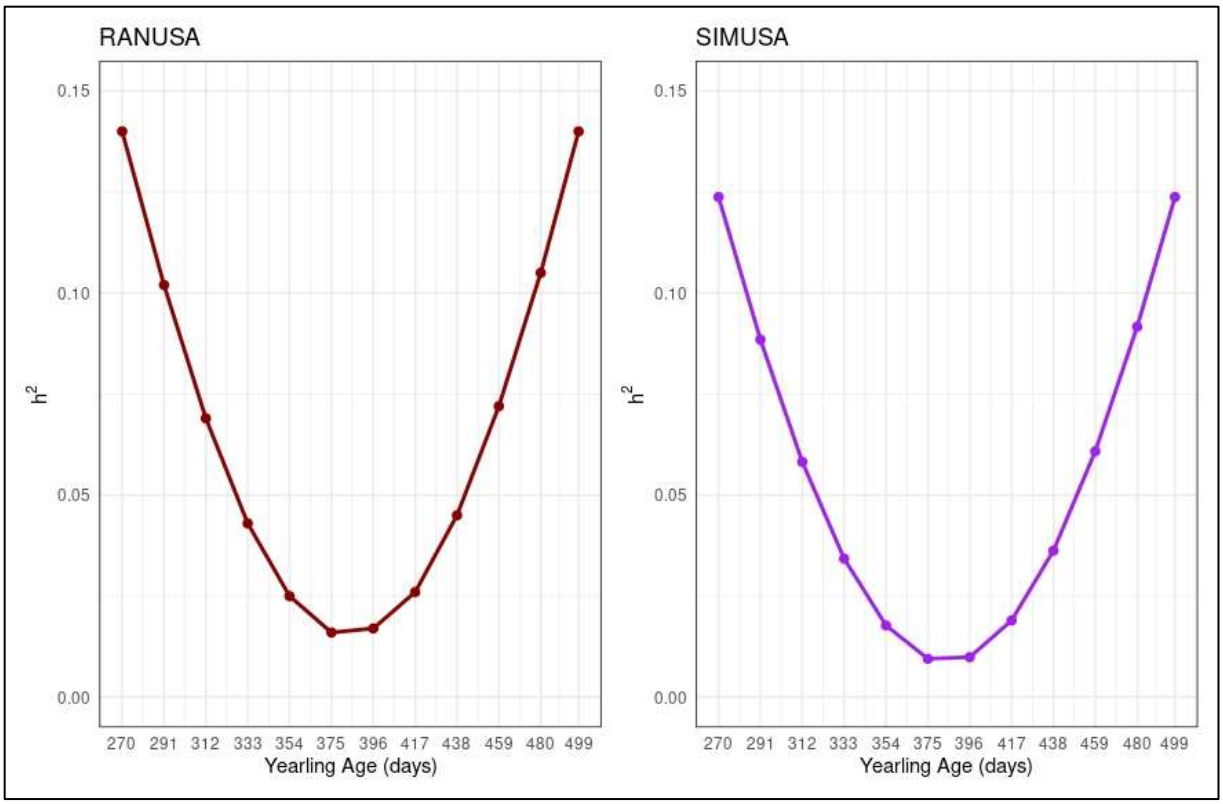

Figure 6.4. Changes in observed heritability estimates for heifer pregnancy (HP) across yearling ages (YAGE) in Red Angus (RANUSA) and Simmental (SIMUSA) heifers.

* The Red Angus population was further subset by setting thresholds on CG size to reduce population size to a more manageable size.

As mentioned before, a common artefact of using Legendre polynomials as the base function in RRM are their sensitivity to changes in data distribution, inflating genetic variances at the beginning and end of data ranges. These models are particularly sensitive reductions in the number of records associated with the covariate implemented (Schaeffer and Jamrozik, 2008). The distribution of YAGE observations for both the RANUSA and SIMUSA populations can be observed in Figure 6.5, where the number of YAGE observations registered at the extremes of the data range may explain the substantial increases in h^2 estimates at the extremely young and extremely old ages when a yearling weight measurement was taken. Both populations distributions appear normally distributed, with the majority of heifers having a yearling weight measurement observed from 350-425 days of age. Though both distributions are more skewed to younger ages, rather than older ages, suggesting many beef producers may be observing

yearling weight at younger ages to coincide with seasonal marketing opportunities. The significant reductions in the number of YAGE coincide with the significant increases in observed HP heritability. Similar trends were observed in h2 estimates in beef cattle (Sanchez-Castro, 2021), and again in dairy cattle for traits like days open and conception rate when implementing RRM (Yin et al., 2012; Brugemann et al., 2013)

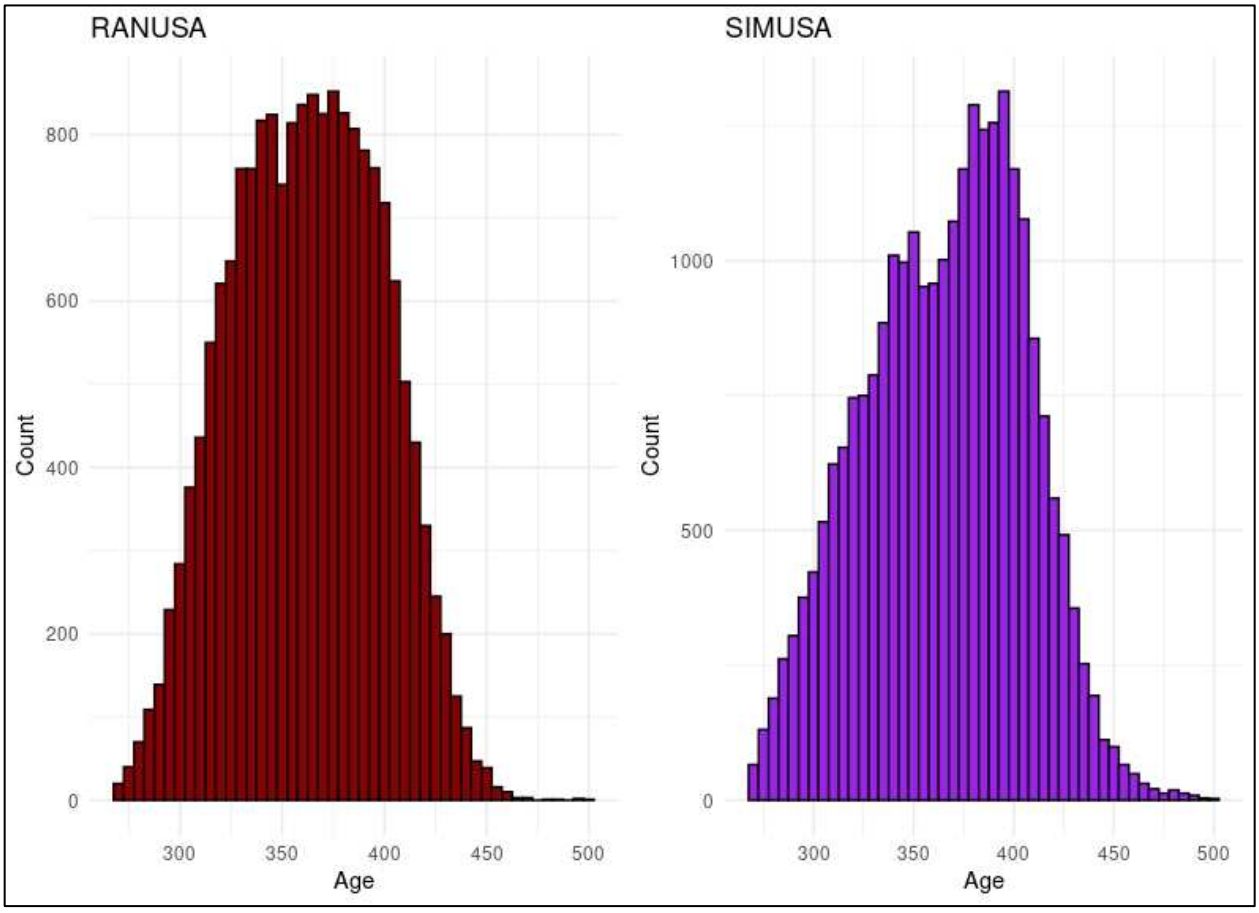

Figure 6.5. Distribution of observed yearling age (YAGE) observations in Red Angus (RANUSA) and Simmental (SIMUSA) heifers.

6.3.2.2 Using age at first exposure as regressed age data

The final RRM analysis was designed to replicate the evaluation methods presented by Speidel et al. (2018) and Sanchez-Castro (2021) to evaluate HP. Despite using the same population definition as in

the HPcw evaluation of subset SIMUSA (Model 5) and the subset RANUSA (Model 6), a greater number of animals were removed due to fewer having an estimate of AFE and in a CG with no variation for the subsequent linear evaluation of HP (Models 9 and 10). Animals were required to have an estimate of AFE and be included in a CG with variation, and since many more of these were removed compared to the HPcs evaluation, the RANUSA (Model 9) and SIMUSA (Model 10) population counts were significantly reduced, limiting statistical power and likely negatively impacting the evaluation as the remaining animals would not be representative of the Red Angus and Simmental breeds. As a result, the variance component estimates of linear HP heritability in RANUSA (Model 9) for the intercept and slope were 0.016 and 0, respectively. The intercept and slope heritability estimates were 0 and 0 in the SIMUSA population (Model 10), respectively. Though the estimate of the intercept from Model 9 is similar to the heritability estimate for the intercept in Angus heifers reported by Sanchez-Castro (2021), a 0 estimate for the slope additive variance results in no variation in observed heritability across different AFE ages. These results appear unusual and may indicate potential issues with the evaluation, or how each population was defined and established. The disparity in linear HP heritability estimates for the intercept and slope in the RANUSA and SIMUSA populations compared to the estimates reported by Speidel et al. (2018) and Sanchez-Castro (2021) warrants further investigation.

Thought the likely root cause for the discrepancies in variance estimates is due to the reduced sample size and subset populations not being representative of the entire breed population, the way in which these data are reported to IGS may be suspect as well. There were many instances of incorrect birth dates in heifers with reported HP phenotypes, which can cause irregularities in the estimate of AFE. By censoring data to animals with a realistic AFE, present in CG with variation, the population structure likely collapsed and the evaluation was not able to isolate genetic differences in the remaining animals. Further analysis into this challenge is required to better understand the potential of RRM for the linear evaluation of categorical HP.

6.4 Conclusion

This study presented different methods for evaluating heifer fertility traits using random regression models in multiple breeds of beef heifers. This study also describes some challenges with estimating an appropriate age estimate for heifers as they near sexual maturity, and notably some of the inherent challenges with different data being reported to global evaluations. While age at first calving appears to be the most suitable age covariate, this requires an assumption of gestation length that potentially introduces error into the evaluation. Yearling age is more readily known in large databases due to a greater number of breeders reporting yearling weight data on heifers; however, estimates of HP at different yearling ages are more difficult to interpret. This is because yearling age can vary significantly across production systems, and interpreting the differences in probability of a heifer becoming pregnant at a non-standardized date seems flawed. It's clear that age at first calving is not an accurate or reliable estimate and may introduce systematic inaccuracies as an age covariate in fertility evaluations.

The findings suggest that while response to genetic selection for heifer pregnancy would be slow due to relatively low or near-zero heritability (in some cases), the development of national cattle evaluations for HP could be possible with these methods. Across breeds, heritability estimates for HP and HPcw were similar in magnitude and had similar trends, suggesting that regardless of breed, the genetic control of genetics of fertility is relatively constant. This means the development of a multi-breed genetic evaluation for HP using RRM is possible. While a traditional linear evaluation of binary HP would be most suitable for implementation in existing genetic evaluations and already developed economic selection indexes, further testing and validation on broader populations must be performed to ensure the correctness and effectiveness of RRM for the prediction of genetic differences in fertility traits.

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CHAPTER 7 - CONCLUSIONS AND IMPLICATIONS

Genetic improvement in beef cattle begins with national cattle evaluations (NCE), which are fueled by central repositories of producer submitted data, which are in turn synthesized into meaningful predictions of genetic merit for economically relevant traits across cattle populations. Heifer fertility is an economically relevant trait, though pregnancy data are cumbersome, untimely to collect, and are considered a rare phenotype in most NCE. Despite this, there are successful examples of existing evaluations for heifer pregnancy (HP) across several beef breed associations. These HP genetic evaluations typically rely on categorical exposure (1 = exposed; 0 = not exposed) and pregnancy outcome (1 = pregnant; 0 = not pregnant) data and involve the use of threshold animal models (TM) to convert these binary observations to an underlying normally distributed range of values known as liabilities. These liabilities are then expressed as a percentage that predicts the likelihood of a bull's daughters becoming pregnant and giving birth as two-year-olds in the form of an expected progeny difference (EPD). However, despite these existing genetic evaluations, little improvement in the genetic trends in HP has been observed. Despite having a genetic evaluation for HP since the early 2000s, the Red Angus Association of America has seen no meaningful improvement in HP genetic trend, with the mean HP EPD in 2000 estimated at +9 and only increasing to +12 in 2020. The American Angus Association also reports a weak genetic trend for HP, with the mean HP EPD in 2000 estimated at +10.8 and only increasing to +11.9 in 2020. Even still, phenotypic trends for HP have observed a decline in average pregnancy rates year over year.

Perhaps the reason for meager improvement in genetic trend is seedstock producers are not placing enough emphasis on HP, or with pregnancy rates already at or near 90%, there is an assumption there is no need for genetic improvement. Additionally, though TM have been successfully implemented in genetic evaluations of HP, a common challenge with the methodology is the inability to evaluate data from contemporary groups that all have the same observation. Even more important is that TM are not

supported in some software used for single-step genomic evaluation. Because of these challenges, this study investigated the development of a multi-breed genetic evaluation for HP by performing a series of HP evaluations using TM, linear animal model (LM), and random regression model (RRM) methods. Data used for this study were provided by the International Genetic Solutions (IGS) genetic evaluation sourced from 9 partner breed associations. Because each breed organization may have its own nuanced definition of HP or differences in how data are reported, inconsistencies in HP data need to be investigated. For example, the American Simmental Association (ASA) does not have an upload format for producers to report HP data but instead uses a system of logic converting whole herd reporting (WHR) codes into HP phenotypes. This study compared variance components and breeding values estimated from various breed populations to try to isolate inconsistencies in data reporting that could introduce errors in a multi-breed NCE.

The first study described the framework for how WHR productivity, enrollment, and culling codes were converted into HP phenotypes and described the relative proportions of reasons why heifers/cows were culled. The proportion of heifers culled due to reproductive failure using this method of establishing HP phenotypes was 14%, which is consistent with the national average. The summary statistics for HP observations were cohesive with other HP observations reported to IGS partner breed organizations. Because of this, this methodology of creating HP phenotypes could be viable and would drastically improve data accumulation as WHR data are more likely to be reported to breed associations and are even mandatory in some organizations. It is worth acknowledging, however, that the ASA does not have a culling code described as “other” which can inadvertently become a catch-all field for producers that are apathetic to data collection integrity. Ensuring this method of data conversion is performed in WHR programs that do not allow for an “other” reason for disposal is imperative.

Once HP phenotypes were established in the ASA population, variance components were estimated using LM and TM methods in that population, along with HP data from the American Gelbvieh Association, the Red Angus Association of America, the North American Limousin Foundation, the American Shorthorn Association, and the Canadian Limousin Association. Evaluations of HP were

performed first within breed before a multibreed population was developed. Heifer pregnancy breed differences were largely negligible, although heterosis was a statistically meaningful factor affecting pregnancy rates. Evaluations using TM were performed across breeds to set a benchmark for comparisons to LM evaluations and to estimate solutions for breed differences and heterosis. Heritability estimates using TM were consistent with the literature and further supported their utility in genetic evaluation, whereas heritability estimates from LM evaluations were considerably lower. However, when cross-validation procedures were performed, LM evaluations had lower estimates of bias and dispersion in breeding values compared to TM evaluations, though admittedly, both evaluations validated well. This suggests that LM evaluations may be a simple and easy alternative for evaluating HP.

While fertility is the primary goal in all beef production systems, there are also economic incentives for heifers to calve earlier in a calving season. For this reason, a series of evaluations for age at first calving (AFC) were tested, which also served as an important investigation as AFC was a potential age covariate in HP evaluations using RRM. This study expanded on literature sources, but a common omission is that few studies appropriately accounted for differences in heifer ages before being first exposed. In many production systems, breeders will mass mate heifers via AI or turn heifers into a breeding pasture at a fixed date. This means that older heifers in a contemporary group will be disadvantaged in having a younger AFC than their younger counterparts if both conceive on the same day. This suggests that AFC is a biased age covariate unless age differences before first exposure are accounted for.

Because of the potential drawbacks associated with LM and TM evaluations of HP, RRM methods were proposed as an alternative. This study aimed at estimating variance components for two separate approaches; the first evaluating HP by the week a heifer calved in her contemporary groups calving window (HPcw), and the second evaluating HP linearly regressed on either a heifer's yearling age or age at first exposure. The evaluation of HPcw showed some potential, as heritability estimates were within literature estimates and were simple to model. However, interpretation of EPD might be

challenging. Additionally, the linear evaluation of HP using RRM primarily resulted in near-zero heritability estimates and was inconsistent with literature estimates using the same methodology.

Results from previous studies suggest there are options for evaluating HP in a multi-breed NCE, but no single method is ideal. While LM evaluations validate well, there is low variance in the EBV for the populations evaluated due to low heritability. The TM evaluations validate well and have reasonable predictions, but they cannot appropriately utilize all available data and are not supported by some modern genetic evaluation software programs. The potential of RRM evaluation methods are evident; however, further evaluation of this methodology must be performed before this approach can be considered.

APPENDIX A

DESCRIPTION OF STANDARDS FOR INTERNATIONAL IDENTIFICATION USED IN GLOBAL OR MULTI-BREED GENETIC EVALUATIONS

In large-scale genetic evaluation, particularly those involving animals from numerous breed populations, proper identification of records is crucial. Animal identification at the breed association level is typically composed of a unique string of alphanumeric characters, usually in sequential order based on date of registration request. In general, nucleus breeders register an animal of a particular breed with the corresponding breed association. These are classified by the "breed association of first registry." However, many breed associations allow the registration of composite animals where the sire or dam may have been previously registered with a different breed association. In this case, due to potential issues with duplicate identifiers a new unique identifier is typically created for the "foreign" parent animal. Every breed association has their own unique way of creating foreign registration numbers. The use of foreign parents is particularly relevant in the North American beef industry with breeders using Angus sires to create designed composites across many different registration entities. For example, the Angus sire TEHAMA TAHOE B767 was first registered with the American Angus Association (AAA) and assigned a registration # 17817177. That same sire is also registered with the American Simmental Association (ASA) with registration # 3396482, the American Gelbvieh Association (AGA) with registration # AMAN17817177, the North American Limousin Foundation (NALF) with registration # AAA17817177, the American Shorthorn Association (ASHA) with registration # xAN17817177, and the Canadian Angus Association (CAA) with registration # 2355349. In summary, this purebred Angus sire has been registered in a total of at least 6 different registration organizations and has progeny in each registry. In a multi-breed genetic evaluation, with each of these breed registries pooling their records, the

ability to correctly assign pedigree relationships relies on a singular unique official entity given to all animals.

Recently, specific guidelines for establishing an official animal identity used in data exchange for multi-breed genetic evaluations have been created. Data provided for this dissertation follows the identification format of the International Committee for Animal Recording (ICAR) guidelines. The identification numbers are 19 characters long, consisting of breed association of first registration (position 1-3), country of first registration (position 4-6), the birth sex of the animal (position 7), and the identification number within the breed association of first registration (position 8-19). Figure A.1 provides an example of an ICAR unique identifier.

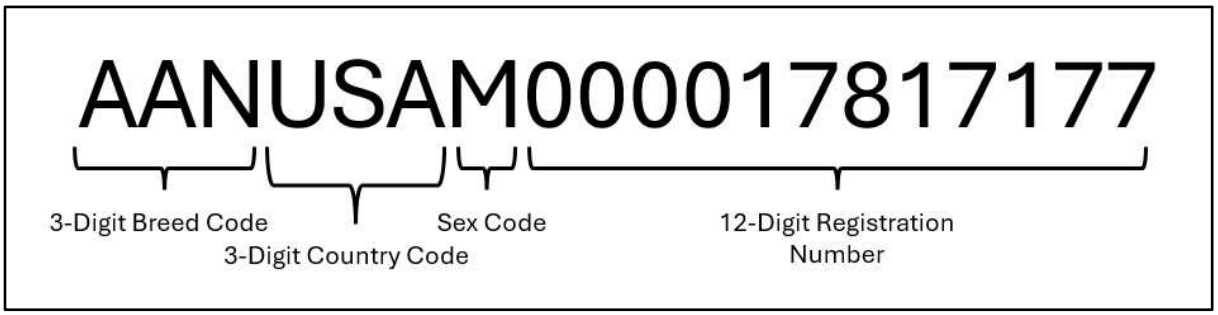

Figure A.1. Example of a unique identifier that follows the guidelines of the International Committee for Animal Recording (ICAR).

Breed codes are defined by the ICAR working group, and the current list contains the most relevant breeds for international use and trade in semen. The breed codes do not inherently identify the "breed" of an animal, but rather the breed association where the animal was first registered. The list of 3-digit breed codes is presented in Table A.1. The international country identifier relies on a 3-letter code in accordance with the International Organization for Standardization (ISO) 3166-1 alpha-3 standards, representing the animal's country of birth. For example, the "United States of America" would have an ISO code of "USA," and Australia would have an ISO code of "AUS." In the case of an unknown country of birth, nationality is defined by the genetic evaluation center, typically the association that first reported

such an animal. Valid sex codes are M = male, and F = female. The animal identifier component relies on the existing first breed association registration number with leading zeros inserted where the official entity is initially less than 12 characters. The 12-character animal identifier can only contain American Standard Code for Information Interchange (ASCII) upper case letters A-Z or numbers 0-9. Spaces, lower case letters, specific coding or non-ASCII characters, or graphic signs cannot be used in the 12-character animal identifier.

For this dissertation's purposes, breed populations were defined using a combination of the registry breed and country codes of the ICAR identifier. Although this approach may result in populations that include multiple breeds, it is more effective at maintaining consistent and robust contemporary groups (CG). Producers with a production system involving more than 1 breed may choose to manage all animals in the same environment and register all animals in a CG with a singular registry service, before selectively registering a few animals with their respective breed associations for sales purposes. By assigning breed population based on the breed association of first registry, and the animal's country of birth, we can maintain larger and more accurate CG.

Table A.1. List of breed names and the corresponding 3-digit breed code used by the International Committee of Animal Recording (ICAR; https://interbull.org/ib/icarbreedcodes).

Breed	Breed Code	Breed	Breed Code
Abondance	ABO	Dutch Belted- Lakenvelder	DBE
Angus	AAN	Limousin	LIM
Aubrac	AUB	Lincoln reds	LIR
Ayrshire	RDC	Longhorn	LON
Bazadais	BZD	Luing	LUI
Belgian Blue	BBL	Rouge des Pres	RDP
Blonde d'Aquitaine	BAQ	Murray-Grey	MGR
Beef Shorthorn	BSH	Montbéliard	MON
Beefmaster	BMA	Marchigiana	MAR
Belgium Red & White	BER	Maremmana	MAE
Braford	BFD	Nellore	NEL
Brahman	BRM	Normandy	NMD
Brangus	BRG	Norwegian Red	RDC
Brand Rood	BRR	Parthenaise	PAR
British Frisian	BRF	Polish White Backed	PBG
Brown Swiss	BSW	Piedmont	PIE
Chianina	CIA	Pinzgau	PIN
Charolais	CHA	Polish Black and White	PZB
Dairy Shorthorn	MSH	Polish Red and White	PZR
Dutch Frisian	DFR	Red Angus	RAN
Eringer	ERI	Romagnola	ROM
Meuse Rhine Yssel	MRY	Salers	SAL
Dexter	DXT	Santa Gertrudis	SGE
Devon	DEV	South Devon	SDE
Dikbil	DIK	Sussex	SUS
Eastern Flanders White Red	BWR	Simmental/Fleckvieh	SIM
European Red Dairy Breed	RDC	Speckle Park	SPK
Gascon	GAS	Stabiliser	STA
Glan Donnersberg	GDB	Swedish Red	RDC
Galloway	GLW	Sahiwal	SAH
Guernsey	GUE	Tarentaise	TAR
Gelbvieh	GVH	Tux	TUX
Groninger	GRO	Tyrol Grey	TGR
Hereford	HER	Verbeter Roodbont	VRB
Highland Cattle	HLA	Wagyu	WAG
Hinterwälder	HWD	Belgium Blue Mixte	WBM
Holstein	HOL	Welsh Black	WBL
Holstein, Red and White	RED	Western Flanders Meat	BRV
Jersey	JER	West-Vlaams Rood	BRD
Kerry	KER	Witrik	WRI

APPENDIX B

ASREML COMMAND FILES FOR RUNNING LINEAR RANDOM REGRESSION MODELS FOR HEIFER PREGNANCY, AND HEIFER PREGNANCY BY CALVING WEEK

Below is the command file for evaluating heifer pregnancy linearly using random regression methods, with Legendre polynomials as the base function. In rare instances, despite obtaining convergence, parameters for variance components would not always estimate at the conclusion of the evaluation, thus !CONTINUE was used as qualifier to resume iteration until parameters were estimated and convergence criteria were met (Gilmour et al., 2009). The VPREDICT statement was utilized to transform the results so estimates of phenotypic variance, heritability of the intercept, and heritability of the linear term could be obtained.

```
Title: Random Regression Model for IGS Red Angus linear (ln) HP... AFE as covariate
id !A !P              # Animal INTid
cg 518 !A                   # Define n of unique CG, !A for alphanumeric values
afe                         # Age at first exposure
hpg                         # Binary heifer pregnancy

ln.ran.stk !ALPHA !MAKE

ranusa.ln.rrm !MAXIT 200 !MVREMOVE !ASUV !AISING !DDF !CONTINUE

hpg ~ cg leg(afe,1) !r leg(afe,1).id

0 0 1                       # Define 1 structure

leg(afe,1).id 2
2 0 US !GPZP        # Fix covariance to 0
0.04
0 0.003

id 0 AINV

VPREDICT !DEFINE
F pheno_var 1+2+3+4 #5
H h2_int 2 5 #6
H h2_slope 4 5 #7

#END
```

Below is the command file for evaluating heifer pregnancy by calving week (HPcw).

```
SIMUSA Random Regression Model for HPcw.... using AFE as age covariate, using leg()
id !A !P              # Animal INTid
cg 2054 !A                    # Define n unique CG, !A for alphanumeric values
afe                           # Age at first exposure
wk                            # Calving Week
hpg                           # Binary heifer pregnancy corresponding to calving at individual wk

sim.rrm.ped.stk !MAKE !ALPHA

simusa.rrm !MAXIT 100 !MVREMOVE !DDF !CONTINUE

hpg ~ cg afe leg(wk,1) !r leg(wk,1).id leg(wk,1).ide(id)

1 1 2 !STEP 0.01    # Define 2 structures (PE and Direct)
445270    # Number of records in data file (44,527 animals w/ 10 entries for weeks calved)

leg(wk,1).ide(id) 2
2 0 US !GP
0.00581
0.00231 0.0096
ide(id)

leg(wk,1).id 2
2 0 US !GP
0.0459
-0.0078 0.0361
id 0 AINV

# END
```

APPENDIX C

CALCULATING OBSERVED HERITABILITY OF HEIFER PREGNANCY, USING A MATRIX OF LEGENDRE POLYNOMIALS EVALUATED AT DIFFERENT CALVING WEEKS

Transforming (co)variances from the evaluation of heifer pregnancy by calving week (HPcw), relies on the formula described in Equation 6.3, similarly presented below:

$$\widehat{G} = \Phi K \Phi'$$

where $\widehat{G}$ was the resulting (co)variance matrix of heifer pregnancy (HP) by calving week (HPcw). Since there were 10 weeks, the order of $\widehat{G}$ was a 10 x 10 matrix to correspond with the number of weeks, with variances on the diagonal, and covariances between weeks on the off-diagonals. Φ is a matrix of order *t x k* containing the orthogonal polynomial coefficients evaluated at *t* standardized calving weeks (WK). Finally, **K** is obtained as the (co)variance matrix of components estimated for the RRM coefficients used in the model, which in this case, are the intercept and linear term. What follows is an example of obtaining the observed heritability for HP by calving week in a population of Red Angus heifers.

Since a first-order polynomial was used to fit HPcw linearly, the order of Φ is a 10 x 2 matrix, with rows corresponding to calving week (weeks 1-10), and columns corresponding to the intercept and linear term (slope). In matrix notation, $\Phi = M\Lambda$ where M was the matrix containing the polynomials of the standardized WK. Λ was a matrix of order *k* containing the coefficients of Legendre polynomials. To obtain M, the Legendre polynomials of the standardized WK span the interval of –1 to +1 and were standardized to a_t. Thus, a_t is the t^{th} WK or age standardized to the interval for which polynomials were defined using Equation C.1.

$$a_t = -1 + 2\frac{(d_t - d_{min})}{(d_{max} - d_{min})} \qquad \text{Eq. C.1}$$

which would result in a *a* vector of order 10 x 1 corresponding to the number of WK, when t=10.

$$a = \begin{vmatrix} -1 \\ -0.7778 \\ -0.5556 \\ -0.3333 \\ -0.1111 \\ 0.1111 \\ 0.3333 \\ 0.5556 \\ 0.7778 \\ 1 \end{vmatrix}$$

The elements of M were then calculated from the formula shown in Equation C.2 shown below:

$$m_{ij} = \left(a_i^{(j-1)},\ i = 1, \ldots t;\ j = 1, \ldots k\right) \qquad \text{Eq. C.2}$$

given that $k = 2$ for the intercept and linear coefficients, and $t = 10$ for the number of standardized calving weeks, M was then:

$$M = \begin{vmatrix} 1 & -1 \\ 1 & -0.7778 \\ 1 & -0.5556 \\ 1 & -0.3333 \\ 1 & -0.1111 \\ 1 & 0.1111 \\ 1 & 0.3333 \\ 1 & 0.5556 \\ 1 & 0.7778 \\ 1 & 1 \end{vmatrix}$$

Next, the matrix Λ of Legendre polynomials coefficients needed to be determined. The procedure to calculate these values was outlined by Speidel et al. (2010) and reviewed in Chapter 2. Since a first-order polynomial was fit in the RRM models then k =2, and Λ was determined as:

$$\Lambda = \begin{vmatrix} 0.7071 & 0 \\ 0 & 1.2247 \end{vmatrix}$$

when $\Phi = M\Lambda$, using simple matrix multiplication then Φ was:

$$\Phi = \begin{vmatrix} 0.7071 & -1.2247 \\ 0.7071 & -0.9526 \\ 0.7071 & -0.6804 \\ 0.7071 & -0.4082 \\ 0.7071 & -0.1361 \\ 0.7071 & 0.1361 \\ 0.7071 & 0.4082 \\ 0.7071 & 0.6804 \\ 0.7071 & 0.9526 \\ 0.7071 & 1.2247 \end{vmatrix}$$

Variances for random effects for this model were estimated for permanent environmental and additive direct effects. Therefore, $\mathbf{K_{pe}}$ and $\mathbf{K_d}$ were obtained from the ASREML .asr file and were of order 2 x 2, with the diagonals being the variances for the intercept and linear term (slope) and the off-diagonals being the covariance between the intercept and slope of each calving week. The (co)variance matrix for $\mathbf{K_{pe}}$ was:

$$\mathbf{K_{pe}} = \begin{vmatrix} 0.1172 & -0.0332 \\ -0.0332 & 0.0299 \end{vmatrix}$$

and the (co)variance matrix for $\mathbf{K_d}$ was:

$$\mathbf{K_d} = \begin{vmatrix} 0.0057 & -0.0053 \\ -0.0053 & 0.0080 \end{vmatrix}$$

Following Equation 6.3, $\mathbf{G_{pe}}$ and $\mathbf{G_d}$ can be computed using simple matrix manipulation and results are as follows:

$\mathbf{G_{pe}} =$

0.1609	0.1445	0.1282	0.1118	0.0955	0.0791	0.0628	0.0464	0.0301	0.0137
0.1445	**0.1304**	0.1163	0.1021	0.0880	0.0739	0.0597	0.0456	0.0314	0.0173
0.1282	0.1163	**0.1043**	0.0924	0.0805	0.0686	0.0567	0.0447	0.0328	0.0209
0.1118	0.1021	0.0924	**0.0827**	0.0730	0.0633	0.0536	0.0439	0.0342	0.0245
0.0955	0.0880	0.0805	0.0730	**0.0655**	0.0580	0.0505	0.0430	0.0355	0.0281
0.0791	0.0739	0.0686	0.0633	0.0580	**0.0527**	0.0475	0.0422	0.0369	0.0316
0.0628	0.0597	0.0567	0.0536	0.0505	0.0475	**0.0444**	0.0414	0.0383	0.0352
0.0464	0.0456	0.0447	0.0439	0.0430	0.0422	0.0414	**0.0405**	0.0397	0.0388
0.0301	0.0314	0.0328	0.0342	0.0355	0.0369	0.0383	0.0397	**0.0410**	0.0424
0.0137	0.0173	0.0209	0.0245	0.0281	0.0316	0.0352	0.0388	0.0424	**0.0460**

$\mathbf{G_d} =$

0.0240	0.0203	0.0166	0.0129	0.0093	0.0056	0.0019	-0.0018	-0.0055	-0.0092
0.0203	**0.0172**	0.0141	0.0110	0.0079	0.0049	0.0018	-0.0013	-0.0044	-0.0075
0.0166	0.0141	**0.0116**	0.0091	0.0066	0.0041	0.0016	-0.0009	-0.0034	-0.0059
0.0129	0.0110	0.0091	**0.0072**	0.0053	0.0034	0.0015	-0.0004	-0.0023	-0.0042
0.0093	0.0079	0.0066	0.0053	**0.0040**	0.0027	0.0014	0.0001	-0.0012	-0.0026
0.0056	0.0049	0.0041	0.0034	0.0027	**0.0020**	0.0013	0.0005	-0.0002	-0.0009
0.0019	0.0018	0.0016	0.0015	0.0014	0.0013	**0.0011**	0.0010	0.0009	0.0007
-0.0018	-0.0013	-0.0009	-0.0004	0.0001	0.0005	0.0010	**0.0015**	0.0019	0.0024
-0.0055	-0.0044	-0.0034	-0.0023	-0.0012	-0.0002	0.0009	0.0019	**0.0030**	0.0041
-0.0092	-0.0075	-0.0059	-0.0042	-0.0026	-0.0009	0.0007	0.0024	0.0041	**0.0057**

where the diagonal elements were the permanent environmental, and additive direct variances for the corresponding WK (weeks 1-10), and the off-diagonal elements were the permanent environmental and additive direct covariances between WK. Therefore, the sum of the residual variances, the permanent environmental variances, and the additive direct variances is the phenotypic variance corresponding to each WK. Heritability for HPcw was determined as the ratio between the additive direct variance to the

phenotypic variance of each WK. Table C.1 summarizes the variances and heritabilities obtained for each WK in this population of Red Angus.

Table C.1. Genetic parameter estimates for heifer pregnancy by calving week (HPcw) obtained from transforming variance component estimates from random regression model coefficients.

Week	Residual Var	PE Var	D Var	Total Phenotypic Var	h^2
1	0.0542	0.1609	0.0240	0.2391	0.1004
2	0.0542	0.1304	0.0172	0.2018	0.0854
3	0.0542	0.1043	0.0116	0.1701	0.0684
4	0.0542	0.0827	0.0072	0.1441	0.0501
5	0.0542	0.0655	0.0040	0.1237	0.0324
6	0.0542	0.0527	0.0020	0.1089	0.0181
7	0.0542	0.0444	0.0011	0.0997	0.0113
8	0.0542	0.0405	0.0015	0.0961	0.0153
9	0.0542	0.0410	0.0030	0.0982	0.0305
10	0.0542	0.0460	0.0057	0.1059	0.0539