THESIS

ESTIMATION OF HETEROTIC EFFECTS ON STAYABILITY IN BEEF CATTLE

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ABSTRACT

ESTIMATION OF HETEROTIC EFFECTS ON STAYABILITY IN BEEF CATTLE

Stayability in beef cattle is defined as the probability that a cow remains in the herd until age six given that she has calved as a heifer. In some breeds with total herd reporting, those cows are required to calve every year. Stayability influences herd profitability by decreasing the need for replacements by increasing the number of cows that reach the typical breakeven age of six. Stayability is a binary trait on the observed scale and is considered a lowly heritable trait. General consensus is that lowly heritable traits should be subject to higher levels of heterosis in crossbreeding programs. Therefore, heterosis should have a positive effect on the cows' ability to remain in the herd until age six. The objective was to estimate maternal and individual heterosis values for stayability. Data was obtained from the American Gelbvieh Association and included a total of 13,114 animals, with 5 being purebred American Angus and 5,493 purebred Gelbvieh, and the rest being a combination of crossbred animals. Variance components and fixed heterosis effects were estimated from single trait animal models using a probit threshold link function. The model included contemporary group as a fixed effect and breed percentage as a linear covariate. Two models were evaluated with different heterosis covariates, model one included only individual heterosis and model two included individual and maternal heterosis. Heterosis was estimated to be 48.96% when individual heterosis is 100% with the first model. For the second model 100% individual heterosis was estimated to be 48.88% and 49.57% was the estimate for 100% maternal heterosis. The results from this experiment indicate that stayability is affected by heterosis and that these effects should be accounted for in cattle evaluation using pure and crossbred data.

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CHAPTER 1: INTRODUCTION

Any beef cattle operation with a goal of profitability, whether formally or informally, likely has a breeding objective that allows them to select on traits that help increase profit margins. In a cow-calf operation, there are several economically relevant traits that can be selected on, one of those being stayability. An operation that has a high stayability or cow longevity rate can decrease cow replacement costs because there is a reduced need for replacements as more cows remain productive for more years.

According to Hudson and Van Vleck (1981), stayability is defined as the probability of a cow surviving to a specific age given they are given the opportunity to reach that age. Stayability has several variations on this definition; in the beef industry the most commonly used is whether a cow remains in the herd until the age of six given she had a calf as a two year old (Brigham et. al., 2009).

Cows that remain in the herd until they reach the age of six have the opportunity to generate sufficient revenue to offset the costs of development and maintenance of both themselves as well as contribute to the recovery of losses associated with cows that fall out of the herd at earlier ages. In order for a cow to obtain a successful stayability observation she has to avoid involuntary culling because of health issues and culling because of poor maternal ability or fertility. Having more mature cows in the herd that reach the six year benchmark means that there is a decreasing need for replacement heifers and therefore there is an opportunity to increase selection intensity placed on heifers when choosing replacements. When fewer replacement heifers are needed there in turn are more offspring that can be sold.

Reproductive performance plays a major role in culling decisions with stayability an indicator of reproductive performance (Martinez et. al., 2005). Stayability is a binary trait on the observed scale, meaning the cow can either receive a successful or unsuccessful observation, and is typically considered lowly heritable. Calving ease and heifer pregnancy are two other reproductive traits that can be expressed on a binary scale and be analyzed with a threshold model for genetic evaluation. K.M. Cammack, et. al., in 2009 reviewed reproductive traits and their heritabilities in beef cattle. There are a total of thirteen reproductive traits that were reviewed, while none of them were stayability or longevity, the heritabilities of the traits that were reviewed are all considered low. According to R.M. Bourdon's *Understanding Animal Breeding* (1996), a trait that has a heritability at or below 0.2, would be classified as a lowly heritable trait which is where reproductive traits tend to lie. Studies have reported heritability estimates for stayability ranging from 0.05 in Angus cattle (Tanida et. al., 1988) to 0.21 in American Simmental and American Gelbvieh cattle (Brigham et. al., 2007).

Through implementation of crossbreeding programs producers can use the effects of heterosis in order to see gains in lowly heritable traits. Heterosis or hybrid vigor is defined as the increase in performance of crossbred animals when compared to that of the purebreds making up that cross (Bourdon, R.M. Understanding Animal Breeding). The effects of heterosis on fertility and survivability traits, which both play a role in a cow's ability to receive a successful stayability observation, can been seen on cumulative weaning weight of calves, Cundiff et. al. (1992), Nunez-Dominquez et. al. (1991), longevity, and first service conception in and Cundiff et. al. (1974).

Stayability is an important trait due to its economic impact on an operation, which will be discussed later. When trying to improve lowly heritable traits, such as stayability, it is easily done by taking advantage of heterosis through crossbreeding. However, the level of the effect of heterosis on stayability is not readily found within the current literature. Nunez-Dominquez et. al. (1991) studied the effect heterosis has on survival or longevity and found that crossbred cattle stayed in the herd 16.2% longer (1.36 years) than straightbred cattle within the same study. With heterosis having an effect on stayability (Nunez-Dominquez et. al. 1991) and other lowly heritable traits (Cundiff et. al., 1974 and Cundiff et. al., 1974) a renewed interest in crossbreeding has occurred. Along with this has come an increased emphasis on a multi-breed evaluation furthered with the merger of numerous breed association datasets for the purposes of genetic evaluation. By working toward an evaluation that takes a more multi-breed approach, the effect heterosis has on certain traits as well as breed differences need to be accounted for. Completing studies such as this one and leveraging other studies on heterosis (Cundiff et. al., 1974, Gregory et. al., 1965, Nunez-Dominquez et. al. 1991, and Cundiff et. al., 1992), is the first step to being able to understand how lowly heritable traits are effected by heterosis and how these effects vary between breeds of cattle. The results can then be used to effectively create a multi-breed genetic evaluation.

Objective

Given the lack of published estimates of the effects of heterosis on stayability, the objective of this study was to estimate maternal and individual heterosis effects for stayability.

CHAPTER 2: LITERATURE REVIEW

Assessing previous literature is important before the start of any study. There are three parts to this chapter, reviews of stayability, heritability, and heterosis. First stayability as a trait is discussed, with general information including how long it has been studied and used within the industry, the varying definitions, and recording definitions. The relative importance of stayability on the economics of a cattle operation is then discussed. This general information is then followed up with a discussion of heritability of stayability along with other reproductive traits. Finally, previous research on heterosis of reproductive traits is discussed. These three topics make up the basis for studying the heterosis effects on stayability.

Stayability

Stayability is a fairly new trait of study, being a topic of research for only the last 30 years (Hudson and Van Vleck, 1981; Van Doormaal et. al. 1985; Tanida et. al., 1988). Stayability has an effect on the total herd dynamic, or the age makeup of a cattle operation as well as the economics of the operation. The Beef Improvement Federation (1990) has defined stayability as the probability of a cow staying in the herd till at least the age of six, making it a prediction of sustained female fertility or at least partially.

Stayability as a Trait

According to Hudson and Van Vleck (1981), stayability is defined as the probability of a cow surviving to a specific age given they have the opportunity to reach that age. The ability of a cow to reach a certain age is dependent on her ability to conceive and give birth to a calf, while avoiding culling for health or other reasons. Because stayability incorporates several culling aspects, most of which deal with reproduction, it is used as an indicator for sustained fertility (Martinez et. al., 2005).

Stayability is a binary trait that is recorded as either a success; calving after the defined stayability cutoff date (e.g. 6 years) or failure; not calving after the designated stayability cutoff date and likely being culled before the cutoff date. Stayability observations are inferred or directly observed when using a total herd reporting system. On a breed-wide scale, total herd reporting and complete animal reporting is a way for breed associations to receive information on all animals within that breed instead of the breeder selectively reporting only the top performing animals. By only submitting data on the best calves in the herd the estimated progeny differences (EPD) for the bulls and cows that those calves are attributed to tend risk being biased (Mallinckrodt et. al. 1995). The case study done by Mallinckrodt et. al. (1995) compared two sires each with ten progeny, sire one's progeny was selectively reported (5 of 10); while sire two's progeny were all reported. The EPD's for weaning weight direct (WWD) for sire 1 and sire 2 were +6 and +12 respectively. If both sires had all of their progeny reported the EPD's for WWD would have been 0 and +20 for sire 1 and sire 2 respectively. Specific to this study, if all calves are not reported to the breed association then the dams of those calves do not get the credit of having produced and raised a calf, meaning that some of the dam may not receive a successful stayability observation when they should have.

There are a few variations in the definition of stayability. Some of these include: stayability to calving, whether a cow has a second calf given that she had a calf as a 2 year old; or stayability to weaning, whether a cow weans a second calf given that she weaned the first calf. These variations are dependent upon the definition of a successful calf: calving or weaning. Another definition, often used in scenarios where total herd reporting is lacking, is merely the presence of that cow at an older age. Most breed associations that use stayability as a trait use the "stayability to calving" definition, with a benchmark of six years, meaning that a dam remains in production at six years of age given that she had a calf as a two year old. Snelling et. al. (1995) defined stayability to calving as whether a cow has a second calf given that she has calved as a two year old. The authors studied four different stayability endpoints 2, 5, 8, and 11 years of age, where the endpoints indicated the number of calves the dam has had, provided she became a dam. After looking at the four different endpoints for stayability it was decided that an endpoint of 5 would be the preferred endpoint in most situations. Five calves would be close to the number required for a cow to break even and would allow the cow to have a sufficient amount of information recorded.

In breeds with total herd reporting (e.g. Gelbvieh, Red Angus, Simmental, Brangus, and Hereford) producers submit a production record every year for each cow that they want to remain "active" in the herd. The production record can be a calf record, a disposal code, or a reason for the cow not having a calf registered (e.g. open, aborted calf, switching breeding seasons). However, if total herd reporting data does not exist, then often a production record is not required every year, although this risks a female having incomplete data or data changing from one year to the next. For example, if a cow calves at 6 years of age, but the calf is not reported, the cow may be assigned an unsuccessful observation, but in the subsequent year, if a calf is registered to her she would then have a successful stayability observation. This can lead to changing EPD in genetic evaluation from year to year.

The varying definitions for stayability result in varying levels of difficulty for receiving a successful stayability observation and therefore differing distributions of stayability observations. If a cow only needs to produce a calf after their first calf at the age of two there will be more cows that are able to achieve a successful observation for stayability as opposed to having to produce a calf every year.

There are several influences on stayability. The most obvious of which is the ability of the cow to remain in the herd for a sustained period of time. In order for a cow to remain in a herd she has to be healthy and productive. Every operation may have a different set of culling criteria but cows that are continually sick, lame or have major health issues are generally culled. Animals that are unproductive are also generally culled, such as animals that continually come up open, continually have calving issues, or do not wean a calf on a yearly basis (Martinez et. al., 2005 and Arthur et. al, 1993) or weaning of below average calves. Both genetic and environmental factors play a role in a cow being able to successfully receive a stayability observation.

Stayability is a trait that measures the longevity of a cow by her ability to remain productive and is therefore use as an indicator for sustained fertility. By looking at reproductive traits that play a role in a cow receiving a favorable stayability observation we can begin to understand the complexity of the trait and what the expected heritability would be, along with how heterosis would affect it. Traits such as age at first calving, heifer pregnancy, scrotal circumference, calving success and first service conception rate are all reproductive traits that play a role in a herd's fertility. Stayability in beef cattle, like most reproduction traits, has been shown to be a trait that is low to moderate in heritability. Even though stayability is not as heritable as other selected traits it is considered to be economically important to cow-calf producers (Brigham et. al., 2009).

Influences on Economics

There are several things that contribute to the profitability of a cattle operation, some of which can be easily controlled by the producer, while others cannot. Some of the influences of profitability are government regulations, feed cost and availability, herd health, and herd genetics, these are broad topics and may not encompass all economic factors in every cattle operation. Government policies and regulations impact the beef industry through: animal health regulations, farm policy, federal lands, food safety and nutrition, international trade, and financial credit (Government Affairs, 2011). Government policies and regulations are not directly controlled by the producer but should be kept in mind when making year to year decisions. Feed cost and availability is another area that the producer does not always have direct or complete control over and can change from season to season or year to year, as it is greatly dependent on climate, grain markets, feed types, location of the producer, and competition for feed resources. Through proper management practices herd health is more easily controlled by the producer by using vaccination schedules, herd health checks, and proper antibiotic usage for treating sick animals (Government Affairs, 2011). The genetics of the herd can be managed by the producer and can be changed through proper selection of cattle and mating selections. For every cattle operation the attributes of the 'perfect' cow may be a different. Producers are able to use EPD's to assess traits that are most important to them and their operation, such as, feed efficiency, calving ease, maternal characteristics, hardiness of climate and beef quality (Gregory and Cundiff, 1980 and Long, C.R., 1980).

One way for an operation to increase profitability is for cows to remain in production longer providing enough time to offset the cost of maintenance and development of the cow as well as cover costs associated with females leaving the herd before they have reached breakeven ages. Under typical market conditions this breakeven point is six years (Snelling et. al., 1995, Doyle et. al., 2000, Garrick et.

al., 2006). The length of the productive life of a beef cow is a trait that is complex and reflects not only her health or ability to avoid involuntary culling but also her fertility, maternal ability, and the ultimate survival of her and her calves (Martinez et. al., 2004).

The average longevity of the herd will influence the overall economic returns of the production system and potentially increase profits as cows remain in the herd longer. There are several reasons for this potential increase in profits all else equal, the most obvious being that by keeping a greater amount of older cows fewer replacements need to be saved, in turn increasing the number of animals that are available for sale (Tanida et. al., 1988). An added benefit to keeping fewer heifers as replacements is that the number of heifers needing development is lower thereby reducing feed and development costs. Having a larger proportion of mature cows in a herd tends to increase total herd production as mature cows have a greater tendency to have fewer instances of calving difficulties. Mature cows are more likely to wean heavier calves as the dams have a lower growth energy requirement, because they are fully developed, and therefore, can use more energy to produce milk (Martinez et. al., 2004, Cundiff et. al., 1992). When there are a greater proportion of mature cows in production the producer has the ability to increase the selection intensity on the replacement heifers, and by keeping fewer calves for replacement heifers the producer has a chance to spread the maintenance costs of the cows over a potentially larger number of calves (Arthur et. al., 1993).

A dairy production system, as opposed to a cow calf operation, focuses on milk production instead of calf production. Even though the focus is shifted, having a greater percentage of mature cows in the herd can improve economic return. Hudson and Van Vleck (1981) were able to show that there is a positive phenotypic and genetic correlation between milk production and stayability within Holstein cattle. Milk production is a large aspect of the Holstein production system, which means that cows that do not have high milk production are typically culled at an earlier age so that young cows do not have the chance to reach later parities. Even with the correlation between milk production and stayability, stayability is not a trait that is typically used as a trait for selection in the dairy industry.

A cow's ability to produce and raise a calf from year to year requires a certain level of reproductive efficiency, which affects the economics of that production system. Enns et al., (2005) found that when there is a 1-unit increase in herd stayability profit also increases by $2500 for those herds that have 40% of cows remaining in the herd until the age of 6. The herds were made up of 1000 cows that had average estimated progeny differences (EPD) within the Red Angus Association of America, while the 14 sires used for mating had stability EPDs that ranged from -2 to 21, which represented the range of stability EPDs for active sires. While profit is the ultimate goal for any production system and having a more mature herd is a way of accomplishing that goal, it does come with some added costs. When there is a larger proportion of the herd that are mature cows the generation interval then increases (Tanida et. al., 1988). As the generation interval increases there is a potential for a reduction in genetic gain per year, however, increasing selection intensity on the replacement heifer will potentially help to offset the genetic loss incurred from an increase in generation interval (Arthur et. al., 1993). As with any drawback the benefits must outweigh the costs and therefore the profit gained from keeping a larger amount of mature cows in the herd must be greater than the cost of having a potential decline in genetic gain per year.

Heritability

Reproductive traits are considered lowly heritable, for example heritability estimate for age at first calving has been reported to be < 0.10 (Smith et al., 1989; Martinez-Velázquez et al., 2003), heritability estimates for first service conception rate are reported to be < 0.10 (Minick Bormann et al., 2006), and heritability estimates for heifer pregnancy can range from 0.20 to 0.30 (Evans et al., 1999; Doyle et al., 2000). Stayability is a considered a reproductive trait and is also lowly heritable. While these heritability estimates for stayability can vary depending on the breed of cattle and the definition of stayability used, estimates are typically below 0.2, as seen in Table 1.

While stayability has been studied for the last several decades, the requirements for a successful stayability observation change depending on the study that was conducted and how strict the culling criteria is. The first three estimates in the Table 1 are from Brigham et al. (2007), and were based on the animal performance records from three breed association herd books; American Simmental (ASA) data from 1959 to 2005, American Red Angus (RAAA) data from 1944 to 2005, and American Gelbvieh (AGA) data from 1959 to 2005. The definition of a successful stayability observation used for the first three estimates (Brigham et al., 2007) was that the cow must stay in the herd and produce a calf at the age of 6 given that she calved as a 2 year old. Having a calf at the age of 6 given first calf was had at 2 or a total of 5 calves is close to the number required for the cow to break even and therefore is a common definition for stayability.

Table 1. Heritability Estimates for Stayability from Literature

Breed	h^2	SE	Definition	Successful Observation	Author
ASA[1]	.21	.010	6 years of age	Having a calf at 6 years of age	Brigham et al, 2007
RAAA[2]	.15	.009	6 years of age	Having a calf at 6 years of age	Brigham et al, 2007
AGA[3]	.21	.010	6 years of age	Having a calf at 6 years of age	Brigham et al, 2007
Angus	.05	.15	Length of life	Length of life from first calf to disposal	Tanida et al, 1988
Herford	.16	.08	Length of life	Length of life from first calf to disposal	Tanida et al, 1988
Canadian Holstein	.059		6.5 years of age	Surviving to a specific age	Van Doormaal et al, 1985
Holstein	.053		6 years of age	Surviving to a specific age given the opportunity	Hudson and Van Vleck, 1981

[1]American Simmental Association herd book
[2]Red Angus Association of America herd book
[3]American Gelbvieh Association herd book

The next two estimates in Table 1 are from Tanida et al. (1988) who also used two different breeds of cattle and an alternate definition of stayability: the length of time from the birth of first calf to disposal. For this study cows were disposed or removed from the herd for any reason associated with no longer being a source of income for the herd, such as physical unsoundness, udder unsoundness, multiple non-pregnancy, calving difficulty, and poor mothering ability. For this study Tanida used two different university herds of cattle. The first herd was the One-Bar-Eleven Angus herd in Wyoming that is managed by Colorado State University, which contained an average of 672 cows plus 110 replacement heifers, first calving was usually at age 2 and there were 7 years of complete cohort groups or birth year groups used. The other was a Hereford herd in Arizona managed by the University of Arizona, which contained an average of 325 cows plus 98 replacement heifers, first calving was usually at age 3 and there were 14 years of complete cohort groups used. A daughter-dam regression was used in order to estimate the heritability for longevity. The differences in the breeds, herd size, herd management and years of available data could all play a factor in the difference in the two heritability estimates.

The next two estimates were calculated in Holstein cattle. The first estimate used Canadian Holsteins from the Canadian Record of Performance in a study done by Van Doormaal et al (1985). The last estimate is from a study conducted by Hudson and Van Vleck (1981) using records from the New York Dairy Records Processing Laboratory. Stayability for these two studies was survival to a set endpoint of 6.5 years and 6 years, respectively. These last two estimates are quite lower than the other estimates reported in Table 1 and could be attributed to the fact that culling criteria for dairy cattle includes milk and milk fat records and thus can be more stringent. Hudson and Van Vleck (1981) saw that there was a positive phenotypic and genetic relationship between milk production and stayability even with stayability having such a low heritability.

As heritability increases the effect heterosis has on that trait typically decreases illustrating the relationship between additive and non-additive genetic effects (Gregory and Cundiff, 1980). Generally stayability has been shown to have a low heritability estimate suggesting that producers can use a crossbreeding system and the effects of heterosis in order to maximize the stayability of a herd.

Heterosis

Richard Bourdon (1996) defines heterosis as the increase in the performance of crossbreds over their purebred counterparts. This increase in performance is from an increase in the gene combination value within the genetic model, where performance or phenotypic value equals the sum of the population mean, the breeding value, gene combination value, and environmental effects. Heterosis is typically most noticeable in lowly heritable traits. Parents pass individual genes to their offspring, allowing for those genes to interact and potentially mask the expression of unfavorable recessive alleles occurring in heterozygous combinations. This interaction of genes is known as gene combination effect. The phenomenon of heterosis has been used extensively in swine and poultry production in order to produce an animal that fits the needs of the consumer (Nordskog and Phillips 1960, Bordas et. al. 1996, Johnson et. al. 1975, McLaren et. al. 1987).

According to the USDA agricultural statistics (2013) 44% of the U.S. beef breeding population involves 90% of the farmers and ranchers; however, they do so with 100 cows or less. With many herd sizes being small, it is important for producers to have a clear production goal and use all the tools available to them and one way to do that could be to use an organized crossbreeding program. EPD's and performance data can be used by producers to choose a breed of cattle as well as individual cows that excel in the traits of interest (e.g. calving ease, weaning weight, or heifer pregnancy) (Gregory and Cundiff, 1980 and Long, C.R., 1980).

There are multiple crossbreeding systems that can be used depending on the desired result and the type of breeding stock that are available for use. Crossbreeding systems can vary in complexity. Four of the simpler systems include two-breed terminal, three-breed terminal, two-breed rotation and three-breed rotation. Two-breed terminal is a system where cows of breed A are bred with bulls from breed B and all of the offspring benefit from 100% individual heterosis and sold. A three-breed terminal system uses cows that are 50% breed A and 50% breed B (normally a cross of two maternal breeds) bred to a bull of breed C and the offspring benefit from 100% individual heterosis as well as maternal heterosis and are sold. A two-breed rotation system is started with cows of breed A mated to bulls of breed B. The offspring (A*B) that are kept for replacements are then bred to a bull of breed A. Offspring from each subsequent breeding season should be bred to the opposite breed of their sire, or to the sire breed to which they are least related. After several generations heterosis stabilizes at about 67%. A three-breed rotation crossbreeding system is similar to the two-breed rotation. The dams would be crossbred and would always be mated to a sire that makes up the lowest percentage of their breed make up. After several generations, heterosis stabilizes at about 86%. Using a cross breeding system provides a way to use nonadditive (heterosis) and additive (breeding value) effects of genes simultaneously (Gregory and

Cundiff, 1980). Selecting the right breeds is important in order to take advantage of breed complementarity in order to meet specific production requirements and marketing situations.

There are three different ways in which heterosis can be captured including maternal heterosis, paternal heterosis and individual heterosis. Individual heterosis is expressed in the individual crossbred animal and its ability to outperform its straightbred counterparts. Maternal heterosis is the increased productivity exhibited by the crossbred female in the form of maternal traits. Paternal heterosis is an increased performance of crossbred bulls with regard to servicing ability in a natural breeding situation (Cundiff et. al., 1992 and Turner et. al., 1968).

Stayability is measured through the productivity of the dams, thus dams receive a stayability observation, and this study will only discuss individual and maternal heterosis. After reviewing relevant literature, the effects heterosis has on stayability have not been previously reported; however heterosis effects on other reproductive traits has been studied. Table 2 shows the effects of maternal and individual heterosis on various reproductive traits.

Table 2. Maternal and Individual Heterosis Effects for Lowly Heritable Reproductive Traits from Literature

Heterosis type	Heterosis effect	Trait	Definition	Author
Maternal	90.9 Kg	Cumulative wwt of calves at 6 yrs	Actual culling[1]	Cundiff et al 1992
Maternal	100.9 Kg	Cumulative wwt of calves at 6 yrs	Imposed culling[2]	Cundiff et al, 1992
Individual	16.2%	Longevity/age at culling	Actual culling[1]	Nunez-Dominquez et al, 1991
Individual	15.8%	Longevity	Imposed culling[2]	Nunez-Dominquez et al, 1991
Individual	12.7%	Conception at 1st service	1st calf at 2 yrs	Cundiff et al 1974
Individual	-.5%	Conception at 1st service	5th calf at 6 yrs	Cundiff et al, 1974
Individual	11.7%	Conception at 1st service	1st calf at 3 yrs	Cundiff et al, 1974
Individual	.3%	Conception at 1st service	5th calf at 7 yrs	Cundiff et al, 1974

[1]Actual culling= culling procedure followed during the experiment
[2]Imposed culling= removing all open cows every year during analysis

The data that was used for all eight of the estimates in table 2 came from a study conducted at the Fort Robinson beef cattle research station in Northwest Nebraska focusing on an extensive crossbreeding experiment started in 1957. The animals that were used in that study included 328 cows born between 1960 and 1963. These included all of the straightbreds and reciprocal crosses of Hereford, Angus, and Shorthorn breeds. Heifers that were not pregnant after their first breeding were culled from the herd. There were two different culling methods that were used to evaluate the study; actual culling which meant that if a cow failed to conceive in two successive years, was seriously sick or injured she was culled. The second form of culling was imposed culling, this was done after the experiment was complete when the data was analyzed, removing all open cows every year, making it a stricter culling method.

Maternal heterosis is the increase in performance of the individual due to the fact that the dam was crossbred. The first two lines in table 2 are both estimates of maternal heterosis for weaning weight analyzed as a trait of the dam. Cundiff et al. (1992) conducted a study, looking at maternal heterosis as it influences cumulative weaning weight of calves. The first two lines in table 2 look at the cumulative weight of calves weaned per initial female at the age of 6. Under the actual culling policy, heterosis for cumulative 200 day weaning weight increased by 90.9 Kg over that of the straightbred dams. Under the imposed culling policy, the heterosis for cumulative 200 day weaning weight increased by 100.9 Kg over that of the straightbred dams in the study. The more stringent the culling constraints showed the bigger the increase in cumulative 200 day weaning weight. However not all cattle operations can afford to use such strict culling criteria and cull all open cows every year.

Nunez-Dominguez et al. (1991) studied the longevity or the age at culling of crossbred dams compared to that of the straightbred dams. The same culling procedures were applied for survival and longevity in the different breeds that were used in the study and the crossbreds. Longevity was defined as lifetime survival, which in this study was the age at which the cow was culled from the herd depending on the culling procedure considered. Nunez-Dominguez et al. (1991) found that the crossbred cows in the herd lived longer. Under the actual culling procedure crossbred cows lived 1.36 years longer than straightbreds, which corresponds to heterosis of 16.2%. Using the imposed culling procedure crossbred cows lived 0.99 years longer than the straightbred cows in the herd, which results in a heterosis level of 15.8%. In this case using a stricter culling method decreased the effect heterosis on longevity because the more culling constraints used, the more cows are culled from the herd at younger ages.

The last four heterosis estimates use conception at first service as the outcome of interest. For a successful stayability observation, a dam must be productive in the terms of producing a calf. The ability of a heifer or cow to conceive at first service can be an indication of that cow's fertility and or ability to recover from the previous partition. These estimates from Cundiff et al. (1974) are results from the second phase of a comprehensive experiment involving Hereford, Angus and Shorthorn cattle that began in 1957 at the Fort Robinson Beef Cattle Research Station in Nebraska. The first phase of the experiment involved reciprocal crossbred and straightbred calves and evaluated the effects of heterosis for preweaning traits, postweaning growth rate, efficiency of growth, weight and age at puberty for heifers, and carcass traits of steers. The second phase of this experiment used the straightbred and reciprocal crosses that were produced in the first phase in order to evaluate the effects of heterosis on reproduction and maternal performance. The heifers for the phase two experiment were split into two management groups; heifers that were managed to calve first as 2 year olds and heifers that were managed to calve first as 3 year olds.

Having heifers and cows that conceive at first service is important to any cattle operation and can help to eliminate the need for higher numbers of clean-up bulls and reduce the range in calving dates. For these heterosis estimates reported by Cundiff et al. (1974), any cow or heifer that was diagnosed as pregnant after one recorded estrus date were considered to have conceived on first service. There were two groups of females that were studied with the first group managed to have their first calf at two years of age and the second a group managed to have their first calf at three years of age. Two heterosis estimates are reported for each group in table 2, representing the 1st service conception resulting in the first calf and in the fifth calf, showing the effect heterosis has on first service conception rates as the females age and continue to be productive in the herd. Heterosis for the two year old management group that conceived during first service was 12.7%. When looking at the same management group in later years, heterosis has a slight negative effect of -0.5% for five year old cows conceiving at first service, meaning they had their fifth calf at six years of age, this could be that the dam was not fully developed at the time of first parturition taking a toll on the dam in later years. The next two estimates are for the group that was managed for heifers to calve first at the age of three. The effect of heterosis on this management group is 11.7%. As with the first management group the effect of heterosis decreased as the cows increased in age. By the time the cows have their fifth calf at the age of seven the effect of heterosis is 0.3% for conception at first service.

Table 2 shows the effects heterosis can have on reproductive traits that are considered lowly heritable much like stayability, thus giving the expectation that heterosis will have an effect on stayability.

Throughout the next chapters, the effects of heterosis on stayability within the Angus, Red Angus, and Gelbvieh breeds will be studied. The probability of a successful stayability observation varies between the three breeds as does the effect of heterosis. While individual heterosis is a main topic of this thesis maternal heterosis is also investigated as it pertains to their daughters staying the herd longer than the daughters of purebred dams.

CHAPTER 3: MATERIALS AND METHODS

Data Description

Herd book data was supplied from the American Gelbvieh Association (AGA) and included animal performance and pedigree records from animals born between 1961 and 2010. The herd book contained information on 1,274,553 animals. The initial data were filtered based on several criteria in the process of constructing the final data set. The edits were applied as follows:

1. Duplicate animals were removed,
2. Individuals had to have all relevant data: parental information, breed percentage, birthdate, calving information, breeder information,
3. The individual animal must have had sufficient age at time of analysis to be eligible to receive a stayability observation (minimum of 2190 days or 6 years),
4. Each contemporary group had to contain at least five animals and show variation in stayability where contemporary group was defined as cow's birth year and the breeder codes for her calves.

The final data set used in this analysis contained 13,114 animals: 7,616, purebred (100%) Gelbvieh, 5, purebred (100%) Angus and 5,493 crossbred animals. Table 3 shows the breakdown of the animals in the final dataset based on breed percentages. Some animals are counted twice in the table depending on the actual breed make up, however they are only included once in the data set and in the subsequent analyses.

Table 3. Number of Animals in Each Breed and Breed Percentage Category

Breed	100%	100%< >75%	75%	75%< >50%	50%	50%< >25%	25%	25%< >0%
Gelbvieh	7616	271	2034	144	2811	116	70	19
Angus	5	5	57	38	1215	51	622	246
Other [1]	0	3	6	30	1571	81	1523	470

[1]Any other breed

Within the data set there were 5,493 crossbred animals which included representations of 21 other breeds of cattle besides Gelbvieh and Angus. In table 4 the 21 breeds are listed representing the "other" category. The majority of the other category is made up of animals that have a percentage of unknown breed percentages.

Table 4. Breeds Included in the Other Category

Breed	Abbreviation	Number in dataset	Percent of dataset
Unknown	UN	5401	83.68%
Hereford (horned)	HH	485	7.51%
Charolais	CH	217	3.36%
Barzona	BA	110	1.70%
Simmental	SM	92	1.43%
Limousin	LM	34	0.53%
Salers	SA	27	0.42%
Hereford (polled)	HP	23	0.36%
Holstein	HO	15	0.23%
Senepol	SE	9	0.14%
Braham	BR	8	0.12%
Shorthorn (beef Scotch)	SS	7	0.11%
	DS	6	0.09%
Red Poll	RP	5	0.08%
Brown Swiss (dairy)	BS	4	0.06%
Chianian	CA	3	0.05%
Jersey	JE	3	0.05%
Amerifax	AM	2	0.03%
Tarentaise	TA	1	0.02%
Shorthorn	SH	1	0.02%
	BH	1	0.02%

Stayability observations were assigned to dams based on their age in days at calving. In order for a dam to receive a stayability observation she was required to calve at two years of age and be at least 2190 days of age (6 years) at the time of calving. Dams that met these requirements received a favorable stayability observation of '1', while dams that did not met these requirements received an unfavorable stayability observation of '0'.

Contemporary groups were formed using cow birth year, and breeder codes for her and her calves, in order to make sure that cows in the same contemporary group were managed together to ensure equal opportunity. Contemporary groups were required to have at least 5 individuals and variation within the group in order to be included in the dataset used to estimate variance components. Contemporary groups with less than five animals and no variation do not add value to the variance component estimate. A pedigree was constructed which included 20,584 animals making up 12 generations prior to animals with observations. There were 1,440 sires and 10,901 dams.

Of the 13,114 animals included in the final dataset, there were 7,529 individual animals with favorable stayability observations to six years of age at the time of calving. The final dataset used for analysis included animal ID, contemporary group, stayability observation, percent Gelbvieh, percent American Angus, degree of individual heterosis, and maternal heterosis expressed in decimal form (0.00 to 1.00). For both individual and maternal heterosis the standard formula was used, (Bourdon, R.M., 1996)

$$Heterosis = 1 - \sum_{i=P}^{n} P_{S_i} P_{D_i}$$

Where n is the number of breeds involved, P_{S_i} is the proportion of breed i in the sire of the individual (expressed as a decimal), and P_{D_i} is the proportion of breed i in the dam of the dam of the individual (expressed as a decimal). The resulting number gives the percent of heterosis for the individual animal expressed as a decimal.

Variance Component Estimation

Variance components were estimated using ASReml3 (Gilmour et al., 2002) using a threshold animal model with a probit link function. Convergence was presumed when the REML log likelihood changed by less than 0.002 in successive iterations, and individual variance parameter estimates changed by less the 1% (Gilmour et al., 2002). Convergence criterion was met after 12 iterations for both models.

Model

Contemporary group was included as a fixed effect along with an individual animal genetic effect (i.e. animal model). Breed percentage, direct heterosis and maternal heterosis were all included as covariates in the statistical model.

Stayability was analyzed on an underlying scale with the following:

$$Y = X\beta + Zu + e$$

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

In the above equations, Y is equal to a vector of transformed observations on the underlying scale, and X is a known design matrix relating fixed effects and covariates to those individuals in vector Y. For this model the fixed effect was contemporary group while degree of backcross and breed percentage, included as a coefficient for each of Angus, Gelbvieh, and other; were fit as linear covariates in vector β. The Z represents a design matrix relating the random additive genetic effects in *u* to the observations in vector Y, and *e* represents a vector of random residual errors. **A** is Wright's numerator relationship matrix. The **I** is an identity matrix with an order equal to the number of observations in **Y**; *and* σ_a^2 and σ_e^2 were additive and residual variances, respectively.

CHAPTER 4: RESULTS AND DISCUSSION

After the final data set was compiled, ASReml3 (Gilmour et al., 2002) was used to estimate variance components in order to estimate heterotic effects between the three purebred breeds and crossbred animals included in the American Gelbvieh Association herd book. The data included 13,114 animals of which 7,529 had successful stayability observations. The data represented 341 contemporary groups with an average of 170 animals/observations per contemporary group.

Two different models were used to determine the effect heterosis on stayability. Model 1 included the observations on Angus animals and Gelbvieh animals with independent variables of contemporary group, breed percentage, and individual heterosis. Model 2 included both breed effects along with individual and maternal heterosis effects. Results from each model are shown separately below.

Along with breed effects the heritability of stayability as a trait was calculated with both models. For model one the heritability estimate was 0.1297 ± 0.015, while for model two the heritability estimate was 0.1295 ± 0.015. In comparison to other heritability estimates from literature with a similar definition of stayability, this is slightly lower. In 2007, Brigham et al., reported heritability estimates for American Simmental, Red Angus, and American Gelbvieh as 0.21, 0.15, and 0.21 respectively. However, in that analysis there was no attempt to account for heterosis or breed differences.

Model 1

Model 1 included the American Angus animals, Gelbvieh animals, contemporary group, stayability observation, breed percentage, and individual heterosis. In addition to breed effects, individual heterosis had an effect on stayability as well. In model 1 individual heterosis is 0.0260 ± 0.1036. When the individual heterosis is 100% the individual is 48.96% more likely to receive a successful stayability observation than an individual with no heterosis.

Stayability has not been widely studied so there are only a handful of studies that have looked at heterosis effects in conjunction with stayability. Nunez-Dominguez et al. (1991) studied longevity or lifetime survival with Hereford, Angus, and Shorthorn cattle, and found individual heterosis increased a cow's life span by 1.36 years over that of the straightbred cows. The 1.36 year increase translates to a 16.2% heterosis effect assuming average purebred cow lifespan is 12 years (Nunez-Dominguez et. al. 1991).

Even though the heterosis effect on stayability has not been widely looked at there have been several studies done on the effect heterosis has on other reproductive traits that contribute to a cow receiving a successful stayability observation. Turner et al. (1968) used Angus, Brahman, Brangus, and Hereford cattle to show that calving percentage increased when using crossbred cattle. The heterosis effect, expressed as a percentage of the parental performance ranged from -2% to 29% with a mean of 14.6% depending on the cross of the cow.

Charles Long (1980) looked at multiple studies that had been conducted evaluating the heterosis effect with beef production in general. The paper discussed characters related to female reproduction and calf survival, measures of size and growth and carcass characters. When looking at characters of the cow related to female reproduction, calf survival and weaning weight there were a total of six cattle breeds used over eight studies over six states. Throughout all of the studies it was found that on average the heterosis estimate for calving rate was 9% above that of the average parental production, and 1% for calf survival to weaning rate. The success of a cow calving and raising that calf is important in order for a dam to remain in the herd and ultimately receive a successful stayability observation.

Model 2

Model 2 included American Angus animals, Gelbvieh animals, contemporary group, stayability observation, breed percentage, maternal heterosis and individual heterosis. In the second model the breed effects for both American Angus and Gelbvieh were the same as in model 1. In model 2 individual heterosis is 0.02789 ± 0.103. When individual heterosis is 100% the individual is 48.88% more likely to receive a successful stayability observation. In model 2, maternal heterosis estimate was -0.0106 ± 0.221 on the underlying scale. When the maternal heterosis of an individual is 100% the individual is 49.57% more likely to receive a successful stayability observation.

Maternal heterosis as it relates to stayability has not been studied to any significant degree. There are other reproductive traits that contribute to stayability in which the maternal heterosis effect has been studied. In 1992, Cundiff et al., reported a study in which the maternal heterosis effect on cumulative weaning weight was evaluated. Three breeds of cattle were used within the study: Shorthorn, Angus, and Hereford. Using a cumulative 200 day weaning weight calves that were born and raised by a cross bred cow were 90.9 Kg heavier than calves that were born and raised by straightbred cows, translating into an 5.8% increase in weaning weight of progeny due to maternal heterosis.

Within most cattle production systems producers tend to keep replacement heifers that were born and raised on their farm. If the producer is taking advantage of individual heterosis for traits such as stayability, the producer can now take advantage of maternal heterosis through the heifers that are kept increasing the chance that their offspring will eventually be able to receive a favorable stayability observation.

Implications

It is important for a cattle operation to use genetic improvement in order to be productive and profitable. There are some traits that are easily selected for and thus are easily and quickly improved. There are also traits that are not as quickly improved upon due to low heritability, long generation interval, or low accuracy of trait measurement. These traits should not be over looked when developing a breeding plan for any cattle operation. One of those traits is stayability.

Stayability is an important trait to a productive cattle operation, however because it is a lowly heritable trait genetic improvement takes longer to be realized. An easy way to improve stayability is to use crossbred animals. When crossbreeding animals, the breeder gets to realize the heterosis gain that comes from maternal and individual heterosis. From this study we can see that heterosis effect breeds differently so some breeds can benefit more from crossbreeding than others when considering stayability.

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