

DISSERTATION

HETEROSIS AND BREED PERCENTAGE EFFECTS ON REPRODUCTIVE
PERFORMANCE AND PREWEANING TRAITS IN A MULTIBREED BEEF CATTLE
HERD IN PANAMA

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Fall 2023

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ABSTRACT

HETEROSIS AND BREED PERCENTAGE EFFECTS ON REPRODUCTIVE PERFORMANCE AND PREWEANING TRAITS IN A MULTIBREED BEEF CATTLE HERD IN PANAMA

Panama is located in Central America and is characterized by a tropical climate. Given the tropical climate conditions, Zebu cattle (*Bos indicus*) are the most predominant breeds in cow-calf systems due to greater resistance to internal and external parasites, and greater tolerance to elevated ambient temperatures and humidity when compared to *Bos taurus* beef breeds. Zebu is a breed that is reproductively inefficient due to Age at First Calving (AFC) being over 36 months and having longer calving intervals (CI), ranging between 12.2 to 26.6 months. The Panamanian cow-calf system reports an average annual birth rate of 55%, with a range of 35% to 60%, depending on the province. This reduced efficiency reported in the cattle production system is also reflected in low kilograms of weaned calves per cow exposed to AI or Bull (80kg to 120 WW/cow exposed), high age at first calving (over 36 months), long calving interval (more than 450 days), and perhaps low-income returns ranging between 8 to 15% per dollar invested. The reproductive efficiency of a herd is one of the main components of a cow-calf system economically. Other important traits that affect the system efficiency and profitability are the preweaning traits: birth weight (BW) and weaning weight (WW). The lack of system efficiency and profitability is why different breeds have been introduced to the country to be used in crossbreeding systems to obtain the benefits of heterosis in growth and reproductive traits. The beneficial effects of crossbreeding on animal performance have been well established, benefiting low heritability traits such as those related to

reproduction. For that reason, in tropical environments, matching the optimum cow numbers with the correct genetic potential in the appropriate production environment can maximize economic benefits. In the tropics, reduced pre- and post-weaning growth and reproductive efficiency are the main limiting factors in the cow-calf system. Prewaning traits are a combination of the direct genetic, maternal genetic, maternal permanent environment, and temporary environmental effects. The challenge for farmers in Latin American countries is to identify those animals that achieve maximum productive performance in a given agro-ecological environment, and to maintain a balance between longevity and generation intervals, in order to obtain the greatest genetic gain per unit of time. Knowledge of the genetic effects of breeds and their crosses in various climatic and forage conditions can be used to identify optimal breed combinations and crossbreeding systems for existing markets.

Based on the heterogeneity of herds in tropical regions due to the introduction of multiple breeds and the different crossbreeding systems utilized, it is necessary to carry out a multibreed evaluation that includes all crossbred and purebred individuals into a single analysis and accounting for the direct and maternal breed and heterosis effect evaluation.

As we mentioned above, different breeds have been introduced in Panamá, but no genetic evaluation program has been developed in the country, to improve the efficiency of cow-calf production. However, it is important to evaluate the breed groups and heterosis effect through productivity indicators to know the relative performance of the breeds and crosses of Zebu and *Bos taurus* cattle in the cow-calf system. Therefore, the objectives of this study were to determine heterosis and breed percentage effects on reproductive performance and preweaning traits in a multibreed beef cattle herd in Panama. For this, traits like age at first calving (AFC), calving interval (CI), gestation length (GL), birth weight (BW), and weaning weight (WW) that constitute

important elements of the breeding objective of beef cattle producers were selected as the traits to evaluate in this study. All the reproductive and preweaning data utilized in this investigation was produced by a multibreed cattle population of the Livestock Experimental Station of Panama Agricultural Innovation Institute (IDIAP) in Gualaca, province of Chiriqui, Republic of Panama. The herd was comprised of the following genetic groups and breed percentage combinations: tropical adapted Brahman (BR), Nellore (Ne), Undefined *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (OTH); crossbreeds (CX), Beefmaster (BF), Three CX (F1 x different BT), R1(Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgraded Brahman (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu). In general, this dissertation was divided into three different studies according to the physiological status of the individual producing the phenotypic record (e.g., calf, heifer, and multiparous cows).

The first study estimated the influence of heterosis and breed percentage on age at first calving (AFC). An animal model was utilized to estimate variance components using data from 619 cows and 1,142 individuals in the pedigree from the multibreed herd with data collected between 2000 to 2019. The average AFC was 42.7 ± 10.5 months, with an estimated regression coefficient for AFC on heterosis of -0.046 ± 0.009 month/percent of outcross. Lower AFC was observed for the F1, R2, and B2, with 39.8 months, 39.9 months, and 39.5 months, respectively. A reduction in AFC was also observed for the Beefmaster (-0.13 ± 0.05 months) and the OTHER category (-0.14 ± 0.04 months). A heritability of 0.17 ± 0.10 was estimated for AFC. These results suggest that heterosis had a beneficial influence on AFC measurements in a multibreed beef cattle herd in Panama.

The second study focused on estimating the influence of heterosis and breed percentage on calving interval (CI) and gestation length (GL), and the correlation between age at first calving (AFC) and CI. Calving performance data included 1,291 repeated observations of CI and GL from 502 cows with a 3-generation pedigree consisting of 2,840 individuals in the pedigree with data collected between 2000 to 2021. A repeated records animal model was utilized to estimate variance components for both CI and GL. Additionally, a bivariate animal model was used to estimate the genetic correlation between CI and AFC. The average CI was 572.6 ± 140 days, and for GL was 284.2 ± 6.3 days, for this population. The regression of CI and GL on heterosis was not significant. A lower CI was observed for the F1, and Three CX, translating to 558.7 days and 567.2 days, which represents 2.3% and 1.3% reduction in CI, respectively when compared to the Zebu group. Calving interval was estimated to be lowly heritable (0.037 ± 0.026), however, a positive genetic trend over the duration of the study. The analysis between CI and AFC revealed a moderate genetic correlation (0.49 ± 0.36) which allows the establishment of a selection program to improve AFC and CI, due to the pleiotropic effect, which would improve the fertility of this multibreed herd in Panama.

Finally, the third study aimed to estimate the influence of heterosis and breed percentage on birth weight (BW) and weaning weight (WW). Data from 900 calves with 2,843 individuals in the pedigree was utilized in a bivariate animal model for BW and WW was utilized to estimate variance components. The estimated regression coefficient for BW on heterosis was not significant, however, for WW was 0.072 ± 0.027 kg/percent of outcross. Lower BW and WW were observed for the Japanese, and B1, while R2 and Upgrade had the highest average WW. Heritability for BW was found to be low 0.14 ± 0.06 and moderate for WW 0.26 ± 0.09 . The proportion of variation of WW accounted by the maternal permanent environment for WW was

0.2 ± 0.09 . The estimated genetic correlation between additive genetic BW and WW was 0.63 ± 0.30 , while a negative, additive genetic correlation was observed for WW and WW maternal -0.43 ± 0.37 . These results suggested that heterosis had a beneficial influence on WW but a limited effect on BW. Additionally, increasing the percentage of WA and BR negatively influenced WW measurements in this multibreed population.

ACKNOWLEDGMENTS

I would like to express my sincere and deep gratitude to my advisor Dr. Scott Speidel for his patience, guidance, and continuous support during my Ph.D. journey. Without his help, this project would have been impossible. I am also grateful for everything you taught me that helped me achieve one of the most important goals of my life.

I also want to express my heartfelt gratitude to my co-advisor Dr. Milt Thomas, for giving me the opportunity to come to this program, so I will always be grateful to you Sir. His mentorship, advice, and continuous support during my graduate career were crucial to keeping me advancing and accomplishing this doctoral degree.

A special thanks to Dr. Mark Enns for his gentleness and continuous willingness to help me in every possible way with my work, as well as with many other difficulties that I faced during my time at CSU.

I would also like to thank Dr. Tim Holts and Dr. Stephen Coleman for their friendship, willingness to teach me, and for serving as my committee members and providing extremely valuable feedback that has significantly enhanced the quality of this research effort.

I also want to express my heartfelt gratitude to Mr. Mark Brown and Ms. Fatima Ahmed for your expressions of love and support throughout my Ph.D. program.

My sincere thanks to Doctors Terry Engle, Shawn Archibeque, and Cait Cadaret for their friendship and guidance throughout this journey.

I would like to acknowledge my bestie – Hilal Yazar Gunes- within the Animal Sciences Department at CSU for her support, friendship, and encouragement to keep going any adversity.

From the bottom of my heart, I want to thank Agata Parsons, Miguel Sanchez, Maria Solis, and Sam Rosado, for their kindness, friendship, and selfless support during my Ph.D journey.

My deepest gratitude to my fellow graduate students within the Animal Sciences Department at CSU (especially for Leeroy, Jonah, Merce, Allison², Taylor, Sara, Carolina, Ghysleine, Kelly, Isabella, Sidney, Lane, Caleb, Levi and Isaac) for their support, friendship, and proving that together we are stronger.

Lastly, but not least, I would like to acknowledge the Panama Agricultural Innovation Institute (IDIAP) and the Panamanian National Secretary of Science and Technology (SENACYT) for giving me the opportunity and the financial support required for my doctoral studies.

DEDICATION

I dedicate this dissertation to my family, especially to my mother Zoila Graciela Murray Blandford and my father Feliciano Gonzalez Canto for encouraging me to always pursue my goals no matter how difficult they seem to be.

I also dedicate this work to my daughter Thais Alexandra and my wife Karina for believing in me even when I didn't believe in myself; for your patience, your strength, and your dedication during all this time that I have been away from home. You are my strength and inspiration to keep going in the most difficult moments. I love you!

To my brothers Edwin, Tanisha and Pedro, for the unconditional support that you have provided to me during all these years and hoping that you always keep in mind that no matter what it costs, you must always fight for your ideals and achieve your goals. To my aunts Ana, Celinda, Majela, Maria, Virginia, Darla and Beatriz and to all my cousins for their unconditional support and prayers.

This dissertation is also dedicated to every friend, colleague and professor that has helped me throughout my graduate career. Collectively, each one of your supporting actions enabled me to always move forward and work hard to overcome any challenge during this journey.

Finally, I dedicate this dissertation to my grandparents Rosa Graciela (RIP) and Pedro (RIP). I know they would be very proud!

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CHAPTER 1 - INTRODUCTION

Panama is located in Central America and characterized as having a tropical climate, with rainy seasons that vary between 6 to 10 months and shorter dry seasons averaging 2 to 6 months depending on the region of the country. Panama is divided into six agroclimatic regions based on precipitation and altitude (Avila,1997, Aguilar et al., 2016).

Livestock in Panama occupies more than 37% of the agricultural landscape and employs more than 20% of the labor force in the rural sector. However, measures of cattle performance indicate low production efficiency reflected mainly in their reproductive ability, with reported average annual calving rate of 55%, ranging from 35% to 60% (INEC, 2020).

In 2021, the Panama cattlemen association (ANAGAN) annual report stated that this low reproduction ability in herds was due to environmental effects, specifically, the niño phenome reported between 2014 to 2016. This low efficiency drives the cattle production system to low-income returns ranging between 8 to 15% per dollar invested.

Given the tropical climate conditions, Zebu cattle are the most predominant breeds in cow–calf systems, but tropically adapted *Bos taurus* breeds such as Senepol and Creoles (Guaymi and Guabala) also exist. Crossbreeding systems (*Zebu x Bos taurus*) have been widely used to obtain the benefits of heterosis in growth and reproductive traits. Heterosis was defined by Dickerson (1973) as the difference in phenotype between the mean of the F1 crossbred offspring and their purebred parents. This is expressed as mid-parent heterosis or the superiority of the F1 cross over the mean performance of the two parents. Also, the greater the differences between the parent breeds, the greater the heterosis effect, especially in low heritability traits (Schiermiester, et al., 2015). Bourdon (2000) stated seven criteria to evaluate any crossbreeding system. These criteria include the merit of component breeds, hybrid vigor, breed complementarity, consistency of

performance, replacement considerations, simplicity, and accuracy of genetic prediction. Depending on the production system and the objective, those criteria can change or vary in importance.

The three main heterosis effects are individual, maternal, and paternal heterosis. Individual heterosis is the advantage of the crossbred individual relative to the average of the purebred individuals, while maternal heterosis refers to the performance improvements to the entire system because of crossbred cows. Paternal heterosis is the differences in performance due to a crossbred sire (Bourdon, 2000).

Another effect gained with crossbreeding is complementarity. This refers to an improvement in the overall performance of offspring resulting from mating (crossbreeding system) which can involve one trait or many numbers of traits (Bourdon, 2000). Many breeds have strengths and weaknesses for key traits that result in different merit whether used in dam or sire crossbreeding roles. The basis of complementarity is that dams and sire do not equally influence the performance of offspring because they are produced, reared, and nurtured by dams (Hammack et al.;2003, 2009).

One of the greatest advantages of heterosis and complementarity is derived from improved reproductive performance and subsequent longevity of the beef cow. Parish (2012) stated that cross-bred cows tend to have greater calf survival rates and greater calf weaning weights. This difference in performance can result in significant economic heterosis, defined as the difference in farm profit between the crossbreed herds and the average of the straightbreed herds (Lopez-Villalobos et al., 2002).

As mentioned above, different breeds have been introduced in Panamá, however non genetic evaluation program has been developed in the country. The challenge for farmers in this

country is to identify those animals that achieve maximum productive performance in a given agro-ecological environment (Elzo y Borjas 2004; Martínez et al., 2008), while maintaining a balance between longevity and generation intervals, in order to obtain the greatest genetic gain per unit of time (Perotto et al. 2006). According to Michael et al., (2022), knowledge of the genetic effects of breeds and their crosses in various climatic and forage conditions can be used to identify optimal breed combinations and crossbreeding systems for existing markets.

When combining information from different breeds, it is important to account for extraneous variation that may have an impact on the evaluation of purebred and crossbred animals. Sources of variation within a breed may include selection strategies and intensity, genetic trends, and breeding philosophies by individual producers (Kuehn et al., 2009; Brown et al., 2010). In multibreed herd populations, crossbred animals serve as a link between the parental populations of pure breeds, thus generating a simple multibreed population composed of pure and crossed animals. Data from these populations should be analysed using multibreed procedures, which take into account additives and non-additives genetic effects, as well as the heterogeneity of variances and covariances within purebred and crossbreed groups (Vergara et al., 2010). Therefore, it is important to define genetic grouping strategies that help account for variability within and between breeds. Due to inherent management and selection practices, not all genetic groups may be represented across herds. As such, including genetic groups as random effects aids in avoiding potential issues related to bias, estimability, and low accuracy of estimates associated with small genetic groups (Schaeffer, 1994). For those aspects, the proposed models for genetic evaluation in multibreed populations (Elzo and Famula, 1985; Arnold et al., 1992) involve estimations of additive genetic breed effects, which form part of expected progeny difference (EPD) used to compare animals of different breed composition. Use of algorithms to account for differences in

groups going through different levels of selection (Westell et al., 1988; Van Vleck, 1990) has been recommended to account for differences in breeds and to reduce costs of solving equations corresponding to genetic grouping. Additive multibreed predictions would help maximize additive genetic progress, and total multibreed predictions would maximize the phenotype of animals produced from intrabreed matings (Elzo, 2011).

Multibreed models have been used to estimate genetic components for different economically important traits going from tick tolerance, adaptive, growth, and reproductive performance (Pragaya et al., 2005). The reproductive efficiency of a herd is one of the main components of the economic and productive performance of a cow-calf system (Prayaga et al., 2009, Berry et al., 2014; Cooke et al., 2020). Other important traits that affect system efficiency are preweaning traits, birth weight (BW) and weaning weight (WW). According to Theunissen et al., (2013), many beef producers derive their income from the total weight of weaned calves. This income can be maximized if we match the optimum numbers of cows with the correct genetic potential in the appropriate production environment (Correa et al. 2006; Burrow, 2012). According to Bourdon (2000) the growth of an animal is influenced by genetic and non-genetic factors, and in the tropics reduced growth is the main limiting factor among other factors such as reproduction in cow-calf systems (Jones and Hennessy 2000).

To improve the efficiency of calf production in Panama, it is important to evaluate the breed groups and heterosis effect through productivity indicators to determine the relative performance of the breeds and crosses between Zebu and *Bos taurus* cattle in the cow-calf system. Therefore, the objectives of this study were to determine heterosis and breed percentage effects on reproductive performance and preweaning traits in a multibreed beef cattle herd in Panama.

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CHAPTER 2 - LITERATURE REVIEW

2.1 General Aspects of livestock in Panama

2.1.1 Agroclimatic condition

Panama is located in Central America and is characterized by a tropical climate with a rainy season that varies between 6 to 10 months in length and a dry season varying between 2 to 6 months in length, depending on the region of the country. It has a tropical rainforest climate along the border with Costa Rica and Colombia and changes into a monsoonal climate in the west. In Panama, days are generally hot, and nights are much cooler. According to the geography, the temperature can change, but on average ranges from 32 degrees Celsius (90° Fahrenheit) during the daytime to 21 degrees Celsius (70° Fahrenheit) at night. However, on the Pacific side, it is common during the dry season to register average temperatures over 36 degrees Celsius (96.8° Fahrenheit). In mountain areas, the average annual temperature ranges from 10°C to 19°C (50-66°F). Humidity is always very high, at about 80%.

The country is divided into six different agroclimatic regions based on precipitation and altitude (Avila,1997, Aguilar et al., 2016). Zone 1 has more than six months of drought with an average precipitation of 1,500 mm of rain and an elevation less than 100 meters above sea level. This zone includes the coastal plains of Herrera, Los Santos, Cocle, and Panama Oeste.

Zone 2 has an intermediate drought, with a range of precipitation between 100 mm to 200 mm of rain during the 4 to 5 drier months. Annual rainfall ranges from 1500 to 3000 mm, and elevations are between 100 mm to 400 meters above sea level.

In zone 3, the drier period is less than 4 months, with rainfall of 200 mm. The annual rainfall ranges between 2,000 and 3,000 mm, with a variety of altitudes between 200 to 500 meters above

sea level. This zone encompasses the Pacific side of Veraguas, Cocle, Panamá, Darien, and most of the province of Chiriqui. Zone 4 is characterized by a short dry period, averaging 300 mm of rainfall during the four drier months, while the average annual is over 4,200 mm at elevations between 500 and 1000 meters above sea level. This zone is distributed through the northern area of Chiriqui and Veraguas provinces. Zone 5 comprises the highlands of Chiriqui with an altitude over 1,000 meters above sea level and annual precipitation over 4,500 mm. Finally, zone 6 is distributed along the Atlantic side of Panama. It is characterized by a non-specific dry period with annual precipitation ranging from 4,500 mm to over 5,000 mm. The elevations in this zone vary from sea level to 1,500 meters above sea level.

2.1.2 Production and reproductive statistics of livestock in Panama

Livestock in Panama occupy more than 37% of the agricultural landscape, and the industry employs more than 20% of the labor force in the rural sector. However, measures of cattle performance suggest low production efficiency, which is mainly reflected in their reproductive ability. The reported average annual birth rate is 55%, with a range from 35% to 60% (INEC, 2020), depending on the province.

From 2014 to 2020, there was evidence of a decrease of 7.6% in the total number of cattle in Panama, falling from 1,603,000 to 1,505,000 head (INEC,2020). In this annual report published in 2021, The Panama Cattlemen Association (ANAGAN) cited the environmental factor of the niño phenomenon that was reported between 2014 to 2016. The reduced reproductive performance of the herds drove a reduction in cattle prices and the increased prices paid for rice and corn crops. This reduced efficiency reported in the cattle production system is also reflected in low kilograms

of weaned calves per cow exposed to AI or Bull (80kg/weaned/calves to 120kg/weaned/calves), high age at first calving (over 36 months), long calving interval (more than 450 days), and perhaps low income returns ranging between 8 to 15% (Guerra, 2013).

2.2 Crossbreeding strategies for tropical environments

Tropical zones have environmental conditions that limit the productive and reproductive performance of *Bos taurus* breeds specialized for milk or beef production. Given the tropical climate conditions, Zebu cattle are the most predominant breeds in cow–calf systems. Tropical adapted *Bos taurus* breeds such as Senepol and Creoles also exist, however, crossbreeding systems have been widely used in order to obtain the benefits of heterosis in growth and reproductive traits. Heterosis was defined by Dickerson (1973) as the difference in mean phenotypic performance between the F1 crossbred offspring and their purebred parents. This is expressed as mid-parent heterosis or the superiority of the F1 cross over the mean performance of the two parents. Also, the greater the differences between the parent breeds, the greater the heterosis effect, especially in lowly heritable traits (Schiermister et al., 2015). Bourdon (2000) stated seven criteria to evaluate any crossbreeding system. These criteria are the merit of component breeds, hybrid vigor, breed complementarity, consistency of performance, replacement considerations, and simplicity and accuracy of genetic prediction. Depending on the production system and objective, these criteria can change or vary in importance.

In the tropics, a variety of crossbreeding strategies have been implemented with varying levels of success. The performance of these crosses is dependent on the expression of additive and nonadditive genetic effects. To design an effective crossbreeding strategy, it is important to understand how heterosis varies across different traits, particularly in tropical systems with diverse breeds and environments, as it depends on breed combination and environmental conditions

(Bunning et al, 2019). Rotational crossbreeding using a two or three breed strategy with a *Bos indicus* breed (Brahman, Nellore, Guzerat, for example) as its base breed is widely used in tropical environments, but the majority of the crossbreed cattle are not followed, and specific crossing strategy in commercial herds. In this regard, Olson (1998) stated that to take advantage of heterosis and complementarity, it is necessary to design a proper crossbreeding system to match specific animals from different breeds with superior traits.

One of the most important considerations for using crossbreeding strategy in tropical zones is to maintain fitness and health to obtain improved performance, especially after the first mating, or F1. McDowell (1985) reported a reduction in performance, ranging from 39% to 60%, when two F1 individuals are mated. That is why synthetic breeds play an important role in tropical and sub-tropical environments. The synthetic breed's gene pools vary from 4/8 to 5/8 improved breed (*Bos taurus*) to 4/8 to 3/8 native or tropical adapted breed (*Bos indicus*). Mating synthetic breeds optimizes the additive and non-additive breed's effects (Gregory and Cundiff, 1980).

For tropical and subtropical environments, Burrow (2006) suggests some rules to optimize crossbreeds' performance and to overcome the detrimental impacts of G x E interactions. The first rule states that 25% to 75% of adapted genes are required depending on the severity of the environment, with 100% of adapted genes required when the environment is extremely stressful. Second, to maintain adaptability and take advantage of heterosis, adapted genes can be provided from *Bos indicus* or from some tropically adapted taurine breed (e.g., creoles). Third, to achieve an optimal level of adaptability and productivity, a combination of multiple breed types (e.g. B. indicus, tropically adapted taurine, British, Continental) will provide the best results. Fourth, to ensure enough parasite resistance (ticks and worms) in harsh environments, some level of *Bos indicus* is necessary, and in harsher environments, a greater percentage of *Bos indicus* influence is

needed. Finally, fifth, the harshest tropical environments require adapted genes to comprise between 60% to 100% of an animal's genome. A crossbreeding strategy combining *Bos indicus* and taurine adapted breeds (e.g. Sanga or Criollo) can be utilized to optimize heterosis and maximize productivity. If the percentage of adapted genes required is between 25% to 60%, the crossbreeding program can utilize an adapted taurine composite (e.g. Bonsmara and Senepol) with a *Bos indicus* or *Bos indicus*-derived breed to achieve desired levels of production and adaptation.

Based on these rules, the five most common crossbreeding systems can be applied in tropical environments (Bertram, 2002). These crossbreeding systems include two breeds using rotational, backcrossing, three breed terminal, and composite systems (Bourdon, 2000). Some important criteria to consider before choosing a crossbreeding system are pointed out by Spengler (2007). In that work, the author states that the number of cows, available breeding pasture, labor and management, production and marketing system, and availability of high-quality bulls of various breeds can all determine the success or failure of the crossbreeding system. The technical guidelines of the different crossbreeding systems were discussed by several authors (Bourdon, 2000; Espasadin, 2010; Spengler, 2007) and will be summarized next.

Two breeds: This can be a terminal or rotational system. The choice of system will depend on the goal of the producer. The result of this system an F1 calves; males and females can be sold to feeders or fatteners for slaughter. Another option for obtaining replacement females is through purchasing from other farmers. The F1 individuals benefit from 100% of the possible individual heterosis. This type of system is implemented in environments where the females of a pure breed are adapted and can be crossed with bulls of another breed (likely non-adapted *Bos taurus*), resulting in progeny with high levels of heterosis for growth, carcass, feed conversion, and

efficiency characteristics. A weakness of this system is the lack of replacements, perhaps, farmers need to buy pure blood heifers from other farmers.

Rotational System: These systems usually refer to a sequence of breeds where males of one or two breeds are used for breeding female crosses whose breed composition is most unlike their own. This system produces its own replacements and minimizes backcrossing, which will maintain acceptable levels of heterosis. This system can be implemented with two or three breeds. In the three breeds scheme, hybrid vigor will fluctuate until approximately the seventh generation, when breed composition reaches equilibrium. On this, Bourdon (2000) stated that is unnecessary to speak of equilibrium in a species with long generation intervals because few rotational systems are likely to remain in place without change for such a long period. This type of crossbreeding allows the heterosis produced generation after generation to be regenerated, which stabilizes at around 67% of that obtained in the F1 if the crossbreeding involves two breeds or 86% when it includes three (Bourdon, 2000; Espasadin, 2005).

Backcrossing: In this crossbreeding system, all the males produced in the F1 are sold for slaughter, while the females (F1) are mated with bulls of one of the two paternal breeds with all the calves produced by this mating sold. This system allows the exploitation of 100% of the maternal heterosis for characteristics such as fertility, milk production, or maternal ability, as well as half of the potential individual heterosis for characteristics linked to the growth of the animals.

Three breed terminal system: This system requires the use of three different breeds. As with backcrosses, all F1 males produced are sold. The F1 females are crossed with bulls of a third breed, and all progeny produced are sold. The main advantage of this system is the exploitation of individual and maternal heterosis, as well as the use of complementarity. The F1 females should be a cross of two maternal breeds that emphasize efficiency and milking ability, while the sire

breed should improve growth rate to efficiently produce progeny (male and female) that are especially desirable from the market standpoint. This produces ample amounts of hybrid vigor, but complementarity is the most important attribute. This system is terminal or static in the sense that breed percentages do not wildly fluctuate over time. In a static system, replacement females have to be produced from a separate purebred population or purchased.

Composite: Composite breeds result from crosses between two or more breeds and are expected to be bred to their own kind, retaining a level of hybrid vigor normally associated with traditional crossbreeding systems (Gregory, 1991; Bourdon, 2000; Weaber, 2015). For a composite crossbreeding system, several subsequent steps depend on the desired production objective. According to Gregory and Cundiff (1999), a series of factors favor the use of compounds. Among them, the simplicity to obtain high and stable levels of heterosis and complementarity between breeds, as well as the possibility of maintaining genetic compositions and optimum additives, especially for production and carcass characteristics. Weaber (2015) stated that when two-, three- or four breed composites are formed, they retain 50%, 67%, and 75% of maximum calf and dam heterosis and improve productivity of the cowherd by 12%, 15%, and 17% respectively.

2.2.1 Heterosis and complementarity effect on performance and reproductive traits

Heterosis is often referred to as "hybrid vigor," measuring the difference between the average performance of crossbred animals and the average performance of the parent breeds that were crossed. This difference must be measured at the same time under the same conditions and is expressed as a percentage of the average performance of the straightbreds. The formula to estimate the percentage of heterosis presented by Olson, (1998), is shown below:

$$\% \text{Heterosis} = (((\text{crossbred average} - \text{straightbred average}) / \text{straightbred average})) * 100$$

The term used to measure crossbreed performance compared to the parental average is hybrid vigor, also referred to as heterosis (Shull, 1914). Shull was the first to propose the word 'heterosis' in 1914. Heterosis results from the increase in the heterozygosity of a crossbred animal's genetic makeup. Heterozygosity refers to a state where an animal has two different forms of a gene. It is believed that heterosis is the result of gene dominance, and epistasis, and the recovery from accumulated inbreeding depression of pure breeds. The level of heterozygosity an animal has depends on the random inheritance of gene copies (Wakchaure et al., 2015). Heterozygosity will result in better performance if there is non-additive gene expression (dominance and epistasis), and the recessive allele results in inferior performance. Dominance is present if the heterozygous individual is not exactly intermediate between the two homozygotes; dominant allele will express over the recessive. According to Buchanan (2011), this is similar to the dominance relationship observed in an offspring from a black bull and a red cow being black with a red mask. In the previous case scenario, the expression of the heterozygous genotype is no different from the expression of the homozygous dominant genotype, having the same phenotypic color (black). In this regard, Evans (2017) stated that non-additive gene effects expressed in a trait are caused by the level of dominance that exists between different genes at a particular location on chromosomes. Meanwhile, epistasis involves gene combinations at one locus interacting with the effects of genes at different loci. It is important to mention that epistasis effects are very complex and are, therefore, very difficult to measure. The largest improvement in animal performance for lowly heritable traits is generated due to heterosis effects, while moderate and little or non-improvements due to heterosis are usually seen in moderately and high heritable traits (Bourdon, 2000; Buchanan, 2011).

There are three main heterosis effects and they are referred to in trade and research literature as individual heterosis, maternal heterosis, and paternal heterosis. Individual heterosis is the advantage of the crossbred individual relative to the average of the purebred individuals, while maternal heterosis refers to the performance improvements to the maternal component of a trait because of crossbred cows. Paternal heterosis is the difference in performance for the paternal component of a trait due to a crossbred sire.

Breed complementarity refers to an improvement in the overall performance of offspring resulting from the mating of two genetically different individuals (crossbreeding system), but have complementary attributes, which can involve one or many traits (Bourdon, 2000). Several breeds have strengths and weaknesses for key traits that result in different merit whether used in dam or sire crossbreeding roles. The basis of complementarity is that dams and sires do not equally influence the performance of offspring because they are produced, reared, and nurtured by dams. Complementarity not only arises from the favorable combination of different types of breeds but also from the way they are combined (Hammack et al., 2003, 2009). Cartwright (1970) stated that complementarity has both a genetic and an environmental component, and it is a cumulative effect on the phenotype due to interactions among phenotypes of the production unit components because it is a characteristic of the breeding system, not of a specific animal.

Complementarity require crossbreeding (Fitzhugh et al. 1975). Fitzhugh and colleagues mention that the use of crossbreeding may potentially provide advantages of both hybrid vigor and complementarity. Hybrid vigor results from the choice of sire and dam based on combining ability and complementarity results when sire and dam are judiciously matched to the production environment. If a successful mating is chosen, the resulting progeny offer greater levels of performance in more traits than their straight-bred parents (Weaber and Spangler, 2013).

Essentially, one would be using the strengths of one breed to offset the weaknesses of another (Gosey, 1991). For example, in low-input or extensive-production systems, an adaptation of breeding females to the production environment is critical. Therefore, the mating of females of indigenous breeds to males of more productive and heavily muscled breeds can increase the value of the offspring while maintaining high levels of adaptation in the breeding females. Additionally, the benefits of having both a well-adapted mother and hybrid vigor often permit the crossbred offspring to perform at acceptable levels and increase overall productivity (Gregory et al., 1982).

One of the greatest advantages of the use of heterosis and complementarity is derived from improved reproductive performance and subsequent longevity of the beef cow. Parish (2012) stated that cross-bred cows tend to have greater calf survival rates and greater calf weaning weights. This difference in performance can result in significant economic heterosis (Lopez-Villalobos et al., 2002). Economic heterosis is defined as the difference in farm profit between the crossbreed herds and the average of the straightbred herds.

On reproductive traits, it is important to establish an effective crossbreeding system with an appropriate breed combination under different environments to exploit heterosis and complementarity. In that sense, under subtropical conditions, Riley et al. (2010) estimated a positive effect of heterosis on age at first conception. This value ranged between -11% to -18% ($P < 0.01$), with calving interval heterosis effects ranging between -9% to 11.6% ($P < 0.01$) for a Romosinuano, Angus, and Brahman crossbreeding system. In Brazil, Perotto et al. (2001) showed a heterosis of -12.8% for age and weight at puberty from hybrid Charolais and Nellore when compared to purebreds. For the same trait, Stewart (1980) reported a -15.8% heterosis effect in a multi-breed population. Mukasa Muguerwa (1989) estimated the age at puberty (first ovulation or estrus) for Zebu in the tropics and subtropics and reported a range of 16 to 40 months, attributing

it to both genetic and environmental factors, including nutrition, disease, temperature, humidity, and season of birth. Age at puberty is an important production trait. Tran et al. (1988) indicated that heifers are selected to calve at 2 years old in order to increase their reproductive life without detrimental effects on longevity or weaning weights compared to those calving at 3 years of age.

Heifer pregnancy has been defined as the probability of a female conceiving at the end of her first breeding season (Crews and Enns, 2008; Boldt et al., 2018). Within *Bos taurus* breeds, the previous definition involves a heifer's ability to become pregnant in order to calve at two years of age (Cammack et al., 2009). In this regard, Cundiff et al. (1974) found a 12.7% increase in first-service conception due to the heterosis effect. The younger age at puberty and heavier weights of crossbred heifers compared to straightbred will allow them to reach a younger age at first calving (Nuñez-Dominguez et al., 1991).

Age at first calving (AFC) is a continuous and easy to measure trait indicating a herd's fertility, and it is related to puberty (Boligon and Albuquerque, 2011; Berry and Evans, 2014; Costa et al., 2019). A genetic improvement program focused on reducing the AFC would offset the cost of raising replacement heifers and therefore, the overall cost of beef production (Cavani et al., 2015). This can also affect the annual genetic progress (Nuñez-Dominguez et al., 1991). Authors agree that the benefit of heterosis on reducing the age at first calving ranges from 10% to 15%. (Vergara et al., 2009; Vieira et al., 2022).

Crossbred dams show greater longevity compared to straightbred dams, which is important for the economic efficiency of the herd. Nuñez-Dominguez et al. (1991) report up to a 16.7% increase in longevity due to heterosis. Lopez-Villalobos et al. (2000), Clasen et al. (2017), and Bunning et al. (2019) estimated that the effect of heterosis on longevity can vary from 2.9% to 35.14% based on the definition of longevity. Longevity is a complex trait that is highly influenced

by production and functional traits as well as other factors like herd management decisions (Berry et al., 2005). Thus, the definition of longevity will vary according to the production system.

Another trait that is highly related to fertility and longevity is Stayability (STAY). This trait represents a measure of sustained fertility through the lifetime of a beef cow and is, therefore, a key driver of beef production efficiency (MacNeil and Vukasinovic, 2011). Stayability has been defined as the ability of a cow to remain in a herd until a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981). More recently, Brigham et al. (2007) defined STAY as the probability that a cow will remain in the herd until 6 years of age, given she first calved as a 2-year-old. From a genetic viewpoint, heritability for this trait varies depending on the age endpoint chosen, the statistical methodology implemented for its estimation, the breed, and the scale in which the trait was analyzed. Heritability for STAY has been shown to range from 0.02 to 0.36 (Snelling et al., 1995; Cammack et al., 2009; Jamrozik et al., 2013; Sanchez-Castro et al., 2019).

2.3 Factors Affecting reproductive efficiency in Cattle.

Reproductive efficiency is influenced by parameters such as age at first calving, calving interval, days open, and service per conception, all of which are summarized as maternal productivity that includes the pre-weaning growth phase of calves (Archer et al., 1998). Reproductive efficiency is highly correlated with total system efficiency of beef production and directly impacts (increasing or reducing) farm profitability (Walmsley et al., 2018). Many factors are related to cow-calf system reproductive efficiency, including genetics and environmental factors. Within environmental factors, the variations in climate conditions, nutritional status, housing, management practices, and any stimuli that demand a response from the animal to adapt to new circumstances could be included (Lee, 1993). Genetic sources of variation include the

natural variability in performance according to the genetic make-up of animals and genetic correlations between reproductive and production traits such as milk yield (Nelson and Beavers, 1982; Drennan and Berry, 2006; Berry et al., 2014).

Under tropical environments with elevated temperature, relative humidity, and solar radiation, low reproductive and productive efficiency has been reported. Combined with nutritional aspects (availability and nutrients of tropical pasture), metabolic and physiological alterations associated with a late age and low weight at the beginning of their reproductive activity, difficulties in achieving cyclical regularity, changes in the duration and intensity of estrus and a low rate of conception and fertility can occur (Hernández et al., 1996). From a genetics standpoint, it is widely documented that *Bos Indicus* and Creoles breeds have a better adaptation to the tropical environments, but lower performance than *Bos taurus* breeds (Nogueira 2004). This is the primary reason to use crossbreeding strategies to improve reproductive and productive performance under tropical environments.

2.3.1 Environmental causes

2.3.1.1 Climate conditions

The environment comprises ambient temperature, humidity, radiation, wind, rainfall, barometric pressure, and ionization (Johnson, 1987). Nonetheless, in a tropical environment, heat stress is one of the major factors affecting cattle performance (Thatcher, 1974). Heat stress may refer to the climate, climatic effects on the cow, or productive or physiologic responses by the cow, and it occurs when the body cannot get rid of excess heat (Lee, 1965). A compounding factor is the fermentation process within the rumen that generates additional heat that cattle need to

dissipate. The effects of hot, humid conditions act in combination and affect the cow's body temperature. That combined effect is known as the temperature-humidity index (THI) (NOAA, 1976; Dewell, 2010). The THI has been used for many years as an environmental management tool for livestock operations during hot weather (Hubbard et al., 1997). There is a range of conditions in which animals maintain relatively constant body temperatures through behavioral and physiological means. That range is termed the thermoneutral zone (Bucklin et al., 1988). In the comfort zone, the energy expenditure of the animal is minimal, constant, and independent of the environment (Nardone et al., 2006). However, extremely cold or hot temperatures increase or decrease the maintenance requirements because homeostasis is disrupted beyond the range of thermoneutrality, compromising reproductive efficiency (Gwazdauskas, 1985). Other consequences of thermal stress are changes in evaporative water loss, increased respiration rate, changes in hormone concentrations, and redistribution of total blood flow (Bucklin et al., 1988). Heat stress' deleterious effects are dependent on the magnitude of the stress, and from the point of view of fertility, it can alter the processes of gonadotropin secretion, oocyte competence, ovarian follicular growth, steroidogenesis, corpus luteum development, uterine endometrial responses, and embryonic growth (Wolfeson et al., 1988; Hansen, 2009; Correa-Calderón et al., 2014; Roth, 2018). Additionally, a negative residual effect on subsequent lactation, reproductive performance, and health has been reported by Collier et al. (1982). This environmental stressor can affect bulls' fertility adversely but with breed differences occurring (Chenoweth et al., 1986). *Bos taurus* bulls have been shown to have lower fertility (lower semen quality) during hot summer months in subtropical regions (Fields et al., 1979; Meyerhoeffter et al., 1985). Zebu bulls in Florida and Texas show little or no adverse effects due to high temperatures during summer months. Elevated body

condition scores can also affect bull fertility. Fields et al. (1979) suggested that overfat bulls are more susceptible to adverse heat effects.

It is important to realize that there is a delayed effect of excessive heat (heat stress) upon spermatozoa, with the damage often occurring 1 or 2 months before major changes are observed in the ejaculate. In that sense, recovery of impaired spermatogenesis following heat stress will often take 60 days or more in bulls (Chenoweth et al., 1986). Sprott (1999) and Sprott et al. (2001) reported negative effects on fertility as dramatic drops in pregnancy rates during warm seasons in places where high humidity was combined with high temperatures.

2.3.2 Nutrition

As stated above, a multifactorial combination involving genetic improvement, inadequate nutrition, poor reproductive management, increased incidence of disease, and poor general cow welfare will all have a negative effect on reproductive efficiency. However, poor nutritional management is, perhaps, the most limiting factor for reproduction (Lucy, 2001, Adams, 1988). In cattle production, good reproductive management is dependent on proper attention to the optimum nutrition of the cow, whose nutrient requirements vary depending on physiological state and specific nutrient demands in order to prevent metabolic disorders (Staples et al., 1990; Boland et al., 2001; Overton and Waldron, 2004). A practical representation of adequate nutrition (combined effects of diet formulation and feeding management) is the body condition score (**BCS**; Staples, 1990). The percentage of body fat at specific stages of a beef cow's production cycle is an important determinant of its reproductive performance and overall productivity (Herd and Sprott, 1986). Body condition scores and rate of body condition gain or loss are important predictors of potential reproductive efficiencies, as most reproductive failures in beef females can be attributed to poor body condition scores resulting from inadequate nutrition (Gearhart et al., 1990). Studies

indicate that cows with lower body condition scores and weight loss have lower conception rates and decreased efficiency of heat detection compared to cows that are gaining weight and have higher body condition scores. Low BCS at calving leads to a delay in the onset of estrus, reduced fertility, and a longer inter-calving period in cows (Williams, 1989; Laflamme et al., 1992).

Changes in body condition score during different physiological stages are a reflection of the energy balance that can influence the endocrine, neural, and metabolic mechanisms. These effects are related to changes in gonadotropic hormone secretion, synthesis, and secretion of progesterone during both the estrous cycle and pregnancy, differential sensitivity of the pituitary-hypothalamus to steroids and releasing hormones, and changes in ovarian activity measured by hormone secretion, follicular development, and ovulation (Blauweikel et al., 1986; Nett, 1987; Short and Adams, 1988; Grummer et al., 2004)

Proper energy management is a key priority for optimizing production and reproduction in dairy and beef cattle. A thin BCS at calving is a result of energy restriction during late pregnancy. This nutritional status will be reflected in an extended interval from calving to first postpartum estrus in beef cows (Richards et al., 1986; Staples et al., 1990; Zula et al., 2002; Lacetera et al., 2005). The magnitude of energy deficiency seems to affect the process of follicular growth and development leading to first ovulation. Ovarian follicles grow and develop for several weeks prior to first ovulation, and the growth of follicles on the ovary is related directly to the animal's energetics balance (Lucy et al., 1992). The link between ovarian function and energy balance is, in part, due to the secretion of luteinizing hormones (LH). This secretion of LH is controlled by the hypothalamus, which detects ovarian secretions and also senses nutritional status (Schillo et al., 1992; Lucy et al., 1992). Cows with the most negative energy balance tend to have the greatest number of small follicles; as energy balance increases, larger numbers of follicles are detected on

the ovary. This movement of follicles in response to energy balance leads to early first ovulation (Lucy et al., 1991).

Prolonged postpartum periods of anovulation (anestrus) greater than 150 days are one of the main infertility problems and are a main factor limiting reproductive efficiency because it prevents the achievement of a 12-month calving interval (Short et al., 1990; El-Sayed et al., 2021). Comparing early postpartum cycling cows with later postpartum cows, De La Sota et al. (1991) found that ovarian follicular development was not similar. Earlier postpartum cows developed large class 4 follicles but secreted less estradiol. This lack of estradiol is also related to the negative energy balance. This author suggested that these oocytes may be less healthy than those of later postpartum with a positive energy balance. Estradiol also initiates the LH surge, which causes ovulation of the oocyte and luteinization of follicle cells forming the corpus luteum. This may explain difficulties in estrous expression, synchronization, and low pregnancy rate.

From the heifer development side, one of the major determinants of the lifetime reproductive efficiency of beef cows is the age at puberty, which is inversely related to nutrition. A targeted body weight of about 66% of their mature weight before their first breeding season represents a minimum level of adiposity and a threshold circulating level of the adipose-derived hormone leptin, which has a central role in the regulation of reproduction in cattle season (Dziuk and Bellows, 1983; Mass, 1987; Patterson et al., 1992). Overall, energy intake is the main factor influencing early-age body weight gain.

Staples et al. (1992) stated that in addition to adequate dry matter and energy balance, it is also important to provide the correct amount of protein, vitamins, and minerals to meet nutritional requirements for optimal productive and reproductive performance. Appropriate nutritional strategies are important to afford beef cattle managers the opportunity to produce beef cattle more

efficiently and become more sustainable (Lucy et al., 1992; Hess et al., 2005; El- Sayed et al., 2021).

2.3.3 Herd health

Herd health is another major factor that influences reproductive performance and herd profitability in beef cattle (Weaver et al., 1987; Ball and Peters, 2004). Five major areas should be prioritized to avoid reproductive losses on the ranch: normal uterine and return of ovarian cyclicity, delayed uterine involution associated with dystocia, retained fetal membranes, metritis, hypocalcemia, and calving complications (Weaver et al. 1987). Erb and Smith (1987) pointed out that other diseases related to the over-conditioning of dry cows can directly affect reproductive performance. These conditions include fatty livers, acetonemia, and delayed conception. Bovine reproductive diseases result in yearly economic losses between \$441 to \$502 million for US beef producers due to decreased production, delayed reproduction, and increased treatment and preventive measurement costs (Bellows et al., 2002). In the United States, the most common reproductive diseases in cattle are brucellosis, leptospirosis, vibriosis, trichomoniasis, infectious bovine rhinotracheitis (IBR), and bovine viral diarrhea (BVD) (Weaver, 1987; Sprott and Field, 1998; García-Ispuerto, 2007). Aono et al. (2013) recommended the implementation of vaccination protocols to improve the reproductive performance of cow-calf systems. Weaver (1992) recommended that reproductive herd programs focus on five primary factors that determine reproductive efficiency: a) length of the post-partum period, b) heat detection, c) conception rate among fertile cows, d) the percentage of infertile cows, and e) abortion rate. Furthermore, the instauration of eradication programs (especially in the case of zoonotic diseases like brucellosis) has proved to be a successful avenue for eliminating those causes of infertility in cattle populations and preserving human health (Zhang et al., 2018).

2.4 Pre-weaning performance and its importance in livestock farming

Growth traits, such as body weight and initial development measures of calves, are important parameters for selection (Baldi et al., 2010). Many beef producers earn their income from the total weight of weaned calves. Net income is derived from the value of calves in the marketplace minus the fixed and variable expenses accrued in their production. This can be maximized when the optimum number of cows with correct genetic potential (size and milk production) is in harmony with the production environment (MacNeil et al., 1988; Burrow, 2006). Besides genetics, system efficiency also plays a key role. In this regard, Archer et al. (1999) stated that the total system efficiency of beef production is highly correlated with cow-calf efficiency, or maternal productivity, as it includes the production of the breeding herd and the preweaning phase of growth.

The weight traits are easily measured and present moderate heritabilities ranging from 0.13 to 0.30 for birth weight (**BW**) and weaning weight (**WW**) and from 0.23 to 0.46 for yearling weight (**YW**) estimated for different breeds (Elzo et al., 1998; Costa et al., 2011; Silva et al., 2012; Mello et al., 2013). The BW is a valuable predictor of dystocia and perinatal mortality in calves, and it also influences a prolonged calving interval (Johanson et al., 2003; Hohnholz et al., 2019). Aside from BW, the selection for heavier weaning weights (**WW**) was also reported to prolong the gestation length (**GL**) and provide a favorable response in age at first calving (**AFC**) (Hwang et al., 2008). Different factors can influence pre-weaning traits in a cow-calf system, which fall into two major categories: environmental factors, and genetics (Vergara et al., 2014)

Environmental effects not only involve climate, management, or nutrition. Santos et al. (2011) mentioned that the birth and weaning weights of calves are influenced by other environmental factors, like the age of the dam at calving. According to this author, the body of the

dam undergoes physiological changes throughout her life, which contribute to better milk production and maternal ability. The maternal-effect, defined as any influence on progeny phenotype that can be attributed to dam phenotype, is an important factor for the development of calves. It includes gestation and lactation periods, milk production, and colostrum quality (Corrêa et al., 2006).

From a genetic standpoint, many studies have been done to improve the growth performance of livestock species through pure breeding (selection) and/or crossbreeding with specialized breeds. The positive effects of crossbreeding on the growth performance of calves and milk production have been reported by Assemu et al. (2015). Finally, Sendeku et al. (2015) concluded that the body weight of calves is strongly influenced by breed, sex, birth type, age of dam, and season of calving.

2.4.1 Environmental factors

2.4.1.1 Agro ecological conditions

Reduced growth performance is the major limiting factor of cattle production in the tropics (Jones and Hennessy, 2000). An animal of good genetic makeup may perform poorly when the production environment is not favorable due to the negative interaction between the animal's genes and its environment (Boitsime, 2006). Agro-ecological zones as described by rainfall, temperature, vegetation type, soil type, and topography, are significant sources of variation in pre-weaning production performance (Bufenning et al., 1982; Dooley, 1982; Ronchiotto, 1993). Season of birth, the interaction between sex and season of birth, and the interaction between agroecological regions and season of birth are important sources of variation in the growth of beef cattle (Boitsime, 2006). Keeping animals in harmony with the environment (adaptability) in which they are raised results

in the maximum utilization of natural resources. Prayaga et al. (2005) defined adaptability as the ability of an animal to survive and reproduce within a specific environment. Under a tropical environment, a marked distinction between *Bos taurus* and *Bos Indicus* breeds is evidenced (McHugh et al., 1997). Zebu breeds are recognized to tolerate harsh tropical climatic conditions, but despite their adaptive advantages, Zebu cattle possess undesirable characteristics such as lower fertility rates and poorer meat quality (Bindon and Jones, 2001). Based on these observations, crossbreeding is evolving as an efficient breeding tool to improve the productive and reproductive performance of largely Zebu breeds under tropical environments.

2.4.2 Genetics factors

To improve efficiency in the cow-calf system., it is important to have the appropriate genetics that match with the environment. Around the world, several studies have been developed to evaluate breed-specific genetic parameters in various environments (Davis, 1993; Meyer, 1992, 1994; Bennett and Gregory, 1996). Therefore, there is a current lack of information on the genetic parameters of growth, adaptive, and temperament traits in cattle populations grazed in tropical environments (Prayaga et al., 2005).

The challenge for ranchers in tropical environments is to identify animals that achieve optimal performance in a given agroecological environment (Elzo et al., 2004a). A common practice is to utilize specialized breeds through the crossbreeding system to increase productivity efficiency and profitability (Vargas et al., 2005).

Genetic evaluation of crossbred populations is very complex. Few studies have reported genetic parameters on pre-weaning and growth traits for multibreed populations (Tosh et al., 1999; Elzo et al., 2004b; Vargas et al., 2005). With the increasing number of crossbred beef cattle

populations, genetic evaluations have become more complex. Few studies have reported genetic parameters on growth traits using multibreed data (Tosh et al., 1999), and even the breed or line-specific genetic parameter information for adaptive traits is very limited (Mackinnon et al., 1991, Burrow, 2001). Although proportions of the non-additive breed genetic effects and the resulting crossbred means are quantified (Prayaga, 2003), implications on the additive genetic variation in these populations and the resulting scope for selection are generally less understood (Meyer et al., 1993).

Genetic prediction systems enable the use of existing breeding values to model total herd productivity (Green, 2009). For crossbreeding, information on breed composition and heterosis are incorporated into multibreed genetic evaluation models to predict phenotypic performance (Cardoso & Templeman, 2004; Pollak, 2006).

Multibreed analysis requires the inclusion of effects for direct and maternal breed additive heterosis (Cardoso et al., 2008; Williams et al., 2010) in addition to epistatic loss and complementarity between different breed effects (Carvalho et al., 2006; Cardoso et al., 2008; Dias et al., 2011). This analysis will permit the comparison of animals of diverse genetic composition (Elzo and Famula, 1985).

Maternal effects reflect the dam's role in providing the environment to survive as well as nourishment for the offspring, starting from uterine development and continuing after birth until weaning (Meyer, 2001; Eaglen and Bijma, 2009) with both a genetic and an environmental component (Falconer and Mackay, 1996). Therefore, in genetic evaluations of maternally influenced traits, the observed phenotypes are often dissected into a direct genetic effect, a maternal genetic effect, a maternal permanent environment effect, and into environmental effects common to siblings (Bijma, 2006; Mrode, 2014; Schaeffer, 2019). Maternal effects can contribute

to the phenotypic similarity of multiple offspring from the same dam, e.g., full-sibs and half-sibs, either arising from the same litter or different parities, and variability between families (Falconer and Mackay, 1996).

Selection for improved maternal performance is often inefficient as it relies on traits often expressed later in life and only measured on females retained in the breeding herd (Cammack et al., 2009). Furthermore, it is important to remember that most reproductive traits tend to be of low heritability, resulting in reduced prediction accuracy and, thus, constraining the rate of genetic gain (Koots et al., 1994; Cammack et al., 2009; Johnston, 2014). According to Robison (1981), the covariance between direct and maternal effects for preweaning growth was generally negative in beef cattle and swine. Based on the above statement, every selection program to increase weaning weight should be designed to keep a balance between direct and maternal genetics potential in the herd.

2.5 Genetic evaluations for fertility traits

Particularly in tropical environments, few beef cattle breeding programs have placed selection pressure on reproduction. Millen et al. (2011) attributed this particularity to the general practice of starting to cycle and rebreed *Bos indicus* heifers at older ages when growth traits are easily measured.

Genetic evaluations for cow fertility are challenging due to the difficulty measuring the phenotype. Some phenotypes are binary in nature, while others can only be measured at an advanced age. This is why different statistical methods may be used, such as multi-trait models applying the best linear unbiased prediction (BLUP) methodology of Henderson (1975), animal

threshold models (TM) (Gianola, 1982), random regression models for longitudinal data (Laird and Ware, 1982), and genomic selection (Meuwissen et al., 2001).

2.5.1 Multiple-trait models (MTM)

Multivariate analyses are a set of statistical methods that allow the simultaneous analysis of multiple traits for each animal. This type of analysis has the ability to simultaneously predict the genetic merit of the animals for two or more traits (Henderson and Quaas, 1976). The key feature of these models is that they incorporate the genetic and residual variances among the traits under study (Mrode, 2014). The way to set up an MTM involves stacking as many single-trait models as the number of different traits needing analysis simultaneously.

Multi-trait analyses can account for the correlation structure among all traits, which increases the accuracy of evaluation. However, this gain in accuracy is dependent on the absolute difference between the genetic and residual correlation, showing that multi-trait predictors resulted in a lower average bias than the single-trait analysis (Mathew et al., 2016).

Persson and Andersson (2004) and Mrode (2014) compared single-trait and multi-trait analyses of breeding values, and they concluded that one advantage of the multi-trait evaluations is that they accounts for culling bias. One disadvantage of multi traits models is the high computing cost.

Genome-wide association studies have been performed in many species with varying degrees of success (Visscher et al., 2012). In general, though, the proportion of genetic variation in complex traits explained by the analyses was usually less than 10% (Visscher et al., 2012). Related to reproductive performance, Pryce et al. (2010), Höglund et al. (2009), Berry et al. (2012), and Hawken et al. (2012) stated that genome-wide association studies exist for dairy and beef cattle. Nonetheless, most genome-wide association studies for reproductive traits suffer from

inadequate statistical power attributed, in part, to the low heritability of the traditional reproductive traits.

When molecular information became available in the form of single nucleotide polymorphisms (SNP), it was of special interest to identify genomic regions associated with particular quantitative traits of economic importance, the so-called "Quantitative Trait Loci" or simply "QTL" (Soller, 1990). In this regard, the superiority of MTM over STM in the mapping of QTL was demonstrated by Jiang and Zeng (1995), who explained that by considering the correlated structure of multiple traits, it was possible to increase the power of detection of QTL. In the same context, authors suggested that QTL mapping using MTM was an effective procedure to test a number of biologically interesting hypotheses concerning the nature of genetic correlations between different traits. More recently, several studies using field and simulated data have demonstrated that the use of MTM for genomic selection based on single-step procedures yielded higher prediction accuracies than their corresponding individual single-step STM procedures (Goddard and Hayes, 2002; Tsuruta et al., 2011, Calus and Verkaamp, 2011; Jia and Jannink, 2012; Guo et al., 2014). Mrode (2005) added that the additional benefit of incorporating genomic information for genetic prediction is the reduction in the generation interval.

2.5.2 Genomics Selection (GS)

Genomic selection (GS) refers to a form of marker-assisted selection in which genetic markers covering the whole genome are used so that all quantitative trait loci (QTL) are in linkage disequilibrium with at least one marker (Goddard et al., 2007). This tool is utilized for the improvement of animals or plants through selection based on evaluations utilizing genomic information. It is a promising tool that may improve the predictive accuracy and genetic gain of fertility traits, improving the production system efficiency (Koivula et al., 2012; Toghiani et al.,

2017) and is now widely practiced across the breeding and genetics industry (Misztal et al., 2009). Genomic selection is one innovation that has revolutionized livestock breeding programs around the world (Van Eenennaam et al., 2014; Georges et al., 2019). The use of genomic information has been shown to substantially increase the rate of genetic gain in many livestock industries where rates of annual genetic gain have more than doubled, especially for lowly-heritable traits (Beavers and Van Doormaal, 2017; Miglior et al., 2017; Brito et al., 2021). Incorporating genomic information into traditional evaluation enables selection for numerous traits that are difficult or expensive to measure (e.g., meat quality, health or disease resistance, carcass quality, and feed efficiency) (Daetwyler et al., 2012; Chesnais et al., 2016; Brito et al., 2017). The increasing availability of marker information in livestock combined with improvements in genomic selection methods allows breeders to select animals based on genotypes early in life. The use of pedigree, phenotype, and genotypic data in combination can increase genetic progress by decreasing the generational interval and by increasing the accuracy of genomic predictions and, thus, the reliability of the assessment of an animal's genetic merit (Koivula et al., 2012). Until November of 2019, genotypes were available for over 3 million U.S. Holsteins, over 700,000 American Angus, and over 100,000 animals per line for some pig and broiler breeding companies (Misztal et al., 2020). Many statistical models have been proposed to predict Molecular Breeding Values (MBV) (Meuwissen et al., 2001; Meuwissen and Goddard, 2004; Gianola et al., 2006). Genomic predictions can be performed by estimating marker effects or by using mixed model equations with genomic relationship matrix **G** (Meuwissen et al., 2001; VanRaden, 2008; Goddard, 2009; Strandén and Garrick, 2009). This type of evaluation can also be performed using random regression SNP marker models (later called **SNP-BLUP**), where the marker effects are estimated

with BLUP, assuming a normal distribution and equal variance for all markers. Subsequently, MBV can be calculated by summing the effects of the alleles across all markers (Goddard, 2009).

Three major methodologies have been used to generate genomic breeding values (GEBV): Two-step genomic selection, Single-step genomic selection, and Single-step hybrid models.

2.5.2.1 Two-step genomic selection

The two-step method is relatively complicated and in its initial form, relies on the existence of animals with highly accurate estimated breeding values (EBVs) from pedigree information. It is also subject to double counting of the genomic information when both parents and progeny are genotyped because the genomic information can be expressed as genomic relationships (VanRaden, 2008)

The two-step genetic evaluations involve the following steps: (i) run a pedigree-based genetic evaluation, (ii) obtain pseudo-phenotypes for genotyped animals such as daughter yield deviations (DYD) deregressed proofs (DRP) or adjusted estimated breeding values (EBV), (iii) calculate direct genomic values (DGV) for genotyped animals using a genomic model based on the pseudo-phenotypes obtained in the previous step, and (iv) combine EBV and DGV for genotyped animals using a selection index methodology.

Two-step genetic evaluations have several drawbacks. These disadvantages include biased or inaccurate predictions for genotyped animals, absence of gain in accuracy for non-genotyped animals, and incompatibility between estimated breeding values for genotyped and non-genotyped animals (Miszta et al., 2009; Patry and Ducrocq, 2011).

2.5.2.2 Single-step genomic selection

Based on the disadvantage of the two step genetic evaluations, Misztal et al. (2009) proposed including both genotyped and non-genotyped animals in a single genetic evaluation by

replacing the numerator relationship matrix ($\mathbf{A}$) with a new covariance matrix ($\mathbf{H}$) that combines genomic and pedigree relationships. With such a matrix, breeding values can be estimated for both non-genotyped and genotyped animals. By doing so, genomic information was incorporated into the classical BLUP methodology, originating what is known as single-step-GBLUP (Legarra et al., 2014; Lourenco et al., 2017). Using selection index principles, Legarra et al. (2009) outlined the procedure to blend the complementary information of molecular markers to the historically recorded and available pedigree data. In parallel, Misztal et al. (2009) detailed the required computational methods to achieve such a combination of information. For their part, and practically at the same time, Christensen and Lund (2010) proposed the same idea (combination of pedigree and DNA markers) from a different perspective based on the imputation of missing genotypes within non-genotyped individuals. A correctly defined joint covariance matrix for non-genotyped and genotyped animals was proposed by Legarra et al. (2009). In consequence, the joint distribution of both kinds of individuals conditional on the observed genotypes is the $\mathbf{H}$ matrix. Matrix $\mathbf{H}$ looks complicated and is completely dense, and its direct inverse is much more difficult than getting $\mathbf{A}^{-1}$. However, Aguilar et al. (2010) and Christensen and Lund (2010) found that the structure of $\mathbf{H}^{-1}$ was simpler than the structure of $\mathbf{H}$ and proposed the algebraic expression. VanRaden (2008) stated that when the number of genotyped animals exceeds the number of markers, and in the presence of clones or monozygotic twins, the genomic relationship matrix is singular. To avoid this, a small fraction of a positive definite matrix of allele frequency is added to $\mathbf{G}$ to ensure its non-singularity in a procedure known as blending. A combined matrix was first shown by Legarra et al. (2009), and complete analysis using the so-called single-step genomic BLUP (ssGBLUP) was presented by Aguilar et al. (2010) and Christensen and Lund (2010), which was shown to be as accurate, if not more than multistep analyses.

Initially, the main focus of the single-step research was ensuring the compatibility of genomic and pedigree information (Vitezica et al., 2011) because incompatibility creates biases, especially under strong selection. Additionally, if a population includes non-genotyped animals with phenotypes, the transition to some form of a single step is unavoidable, because BLUP, which is used to create pseudo-observations adopted in multistep, becomes biased by genomic preselection (Patri and Ducrocq, 2011). The only alternative to ssGBLUP that has been explored is the use of segregation analysis to partially “infer” genotypes of the ancestors of genotyped animals in order to later introduce this information in a refined ssGBLUP (Meuwissen et al., 2016). This strategy showed promising results, but it is computationally complex and has not been pursued.

In order to overcome the potential limitations of single-step procedures due to the increasing number of genotyped individuals, procedures such as the Algorithm for Proven and Young (APY) have been developed (Miszta et al., 2014). Based on Henderson’s (1976b) recursive algorithm implemented to obtain $\mathbf{A}^{-1}$ without explicitly creating $\mathbf{A}$, the APY methodology builds $\mathbf{G}^{-1}$ directly for a subset of the most influential genotyped animals, denoted “core animals”. To do so, APY assumes that the genomic recursions for young animals (non-core individuals) contain coefficients only for proven animals (core individuals). Therefore, it is possible to ignore the relationships among non-core animals in the construction of $\mathbf{G}^{-1}$ at the cost of a negligible impact on the estimation of genomic breeding values (Fragomeni et al., 2015). From a different perspective, an alternative strategy to avoid limitations imposed by the increasing number of genotyped animals is the implementation of methods that do not require computing $\mathbf{G}$ or its inverse, deriving in the development of the single-step Bayesian regression marker effects models, also known as single-step hybrid models (Fernando et al., 2014, 2016).

Consequently, any model utilizing relationship matrices can be fitted using the combined relationship matrix **H**. This means that evaluations using the single-step procedure would not be restricted to simple models (e.g. single-trait models with no maternal components). Rather, the method allows the application of more complex evaluations, such as those performed using multivariate models with maternal components, threshold models, and/or even random regression models (Misztal et al., 2009; Legarra et al., 2014; Kang et al., 2017). Other advantages of the single-step over the multiple-step procedure include the ability of the single-step approach to automatically account for all relatives of genotyped individuals and their performance. Accordingly, increments in the accuracy of predictions are not limited only to genotyped individuals since their non-genotyped relatives also benefit (Christensen et al., 2012). Ultimately, the elimination of the extra evaluation steps helps avoid the loss of information (Legarra et al., 2009).

Despite the great benefits of the single-step procedure, potential challenges and drawbacks have also been acknowledged in the comprehensive review of Legarra et al. (2014). For instance, the method increases the programming complexity to fit complicated marker effects models such as those based on Bayesian regressions. Additionally, given that the nature and assumptions of the method rely on Fisher's infinitesimal model, the single-step procedure does not have a way to appropriately handle QTL with major effects (although this is also a limitation within multiple-step procedures). Furthermore, and perhaps more importantly, since the method explicitly requires the inverse of a dense G matrix, the constantly increasing number of genotyped individuals could eventually reach a limit where the computation of such an inverse would become impossible (e.g. >100,000), threatening the feasibility of this methodology (Fernando et al., 2014, 2016).

Another limitation noted by Lourenco et al. (2020) is based on several parameters (called blending and scaling factors) that may influence the accuracy and bias of single-step GEBV. The values used for these parameters are population-specific, and they need to be defined to optimize the prediction of GEBV (i.e., maximize validation accuracy while reducing bias), especially when inbreeding is not accounted for in the analyses (Tsuruta et al., 2019). However, the models used in ssGBLUP studies include single and multiple-trait models, with or without permanent environmental and maternal effects (Lourenco et al., 2020; Tsuruta et al., 2015), random regression (Oliveira et al., 2019), reaction norm (Zhang et al., 2018), threshold (Bermann et al., 2021), and survival models (Vallejo et al., 2019).

2.5.2.3 Single-step hybrid models

The single-step hybrid model is an alternative computational approach for a single-step model that provides solutions for the marker effects and the imputation errors for non-genotyped animals rather than directly providing the EBVs (Fernando et al., 2014; Garrick et al., 2014). It has computational advantages over Misztal et al.'s (2009) in that it does not require any large matrix inverse, and it has the ability to implement marker selection methods such as Bayes C (or other forms of the Bayesian alphabet). This marker selection approach resulted in a substantial increase in the accuracy of the predictions from the same amount of genotype data, and the breeding values of animals were expressed as the sum of marker effects estimated within the analysis.

A crucial limitation for hybrid models, stated by Misztal et al. (2014), is based on the requirement of storing large intermediate data files corresponding to the imputed Genotypes, as well as the software restrictions to accomplish that task. Nonetheless, the single-step hybrid model is the method of choice for genomic evaluations in most livestock species when not all the animals

in the evaluations have genotypes. The current state of the model allows the implementation of most of the models used in animal breeding for a very large number of genotyped animals. This is possible due to the availability of efficient software packages like BOLT (Garrick et al., 2018). But Varona et al. (2018) hold that applying complex models such as social interaction models or including dominance, epistasis, and genotype by environment interactions is still challenging when the number of genotypes is large. This creates the need to continuously increase efficiency and flexibility. Bermann et al. (2022) stated that different ongoing research aims to make single-step hybrid model an efficient tool for constantly growing datasets. These research topics include an approximation of theoretical accuracies of estimated breeding values, improving convergence of the solving algorithms, increasing the efficiency for categorical traits analysis, and calculating p-values for large-scale single-step genome-wide association (ssGWAS).

2.6 Multibreed Genetic Evaluation

Multibreed genetic evaluations are an extension of the traditional intra-breed genetic models that take into account additive and non-additive effects within and between breeds (Elzo et al., 2004b). In these models, the additive genetic effects result from the combination of additive genetic effects within and between breeds (Vargas et al., 2010). Van Raden (1992) stated that before crossbred information can be included in genetic evaluation, it is necessary to account for heterosis and founder breed effects. In addition, because of the more diverse nature of crossbred progeny in a multi-breed evaluation, variance components, including heritability and genetic correlations, may need to be updated to better describe additive and environmental effects as well as the relationships between purebred and crossbred performance.

In multiracial populations, crossbred animals serve as a link between the parental populations of pure breeds, thus generating a simple multiracial population composed of pure and crossed animals. The data from these populations should be analyzed using procedures that take both additive and non-additive genetic effects into account as well as additive and non-additive effects and the heterogeneity of variances and covariances within purebred and crossbred groups (Vergara et al., 2010). When combining information from different breeds, it is important to account for extraneous variation that may have an impact on the evaluation of purebred and crossbred animals. Sources of variation within a breed may include selection strategies, intensity, genetic trends, and breeding philosophies by individual producers (Kuehn et al., 2009; Brown et al., 2010). Therefore, it is important to define genetic grouping strategies that help account for variability within and between breeds. Due to inherent management and selection practices, not all genetic groups may be represented across herds. As such, including genetic groups as random effects aids in avoiding potential issues related to bias, estimability, and low accuracy of estimates associated with small genetic groups (Schaeffer, 1994).

Elzo (1990) indicated that multibreed mixed model equations are more complex than intra-breed models. The main difference is the heterogeneity of genetic and environmental variances and covariances of the multibreed models. Models proposed for genetic evaluation in multibreed populations (Elzo and Famula, 1985; Arnold et al., 1992) involve the estimation of additive genetic breed effects, which form part of expected progeny difference (EPD), used to compare animals of different breed compositions. The use of algorithms to account for differences in groups going through different levels of selection (Westell et al., 1988; Van Vleck, 1990) has been recommended to account for differences in breeds and to reduce the computational costs of solving equations corresponding to genetic grouping. Additive multibreed predictions would help maximize additive

genetic progress, and total multibreed predictions would maximize the phenotype of animals produced from intra-breed (Elzo, 2011).

To better understand the multibreed analysis, the basic multibreed animal model described by Elzo (2006) will be presented.

2.6.1 Multibreed Animal Model

A multibreed model for a production trait contains the following effects:

- 1) Multibreed contemporary group: These groups are made up of animals of one breed or of multiple breed composition, of similar ages, and of the same sex. They have also been subject to similar handling and feeding conditions.
- 2) Other fixed effects (e.g., age of dam).
- 3) Additive genetic groups: Additive genetic groups would be constructed based on animals with known parents of the parent breeds. If the effects of parental breeds are not estimable, additive genetic effects are estimated as deviations from a multi-breed additive genetic base. This multi-breed genetic base may be made up of animals of one or more breeds and breed groups born in a certain year or within a certain period (Elzo, 1983; Elzo and Bradford, 1985; Elzo and Famula, 1985).
- 4) Nonadditive genetic group: Nonadditive group effects in multiracial populations refer to those associated with interracial and interracial interactions within one locus or at two loci (crossbreed animals). This effect contains the intralocus and interloci interaction effects between genes of one or more breed in each racial group combination. In other word, are defined in terms of the probabilities of having alleles from different breeds at one locus or at two loci in progeny of bulls from one or more breed groups mated to cows from more than one breed group. Due to

confounding effects in the model, intra-locus interracial effects are usually defined as deviations from the mean of intra-locus intraracial effects (heterosis) (Elzo and Wakeman, 1998). Similarly, interracial effects between alleles at two loci can be defined as deviations from the mean of the interracial interactions between two loci (Elzo, 1990b).

5) Animal additive genetic effect: Multibreed additive breeding value predictions allow unbiased comparison of animals of any breed composition within a population. This represents the sum of the additive effects of all genes affecting a trait in an animal as deviation from the multibreed additive genetic base (full in the case of the animal model, half in the case of a sire and sire model or maternal). Multiracial additive genetic effects are not only due to interbreed additive genetic effects but also to interracial additive genetic effects. These additive interracial genetic effects are called segregation effects (Wright, 1968; Lande, 1981; Lo et al., 1993).

6) Animal non-additive genetic effect: These nonadditive random effects are defined as deviations from the nonadditive gene groups for one locus and two loci and represent the maximum value from one parent for each interracial effect. If a sire, or one of his relatives, has all races of the multi-breed population represented in his progeny, the non-additive breeding value of progeny from this sire mated to any dam within the population can be predicted (Elzo, 2006). This effect can be estimated using a subclass (categorical) model or a regression (as a covariate) model (Elzo, 1990).

7) Residual.

In the matrix from Elzo (2006), the basic model for a two trait birth weight (BW) and weaning weight (WW) and two breeds (A and B) effect are defined as:

$$y = Xb + Z_{ga}ga + Z_{gn}gn + Z_a ca + Z_n cn + e$$

$$\begin{bmatrix} y \\ ca \\ cn \\ e \end{bmatrix} \sim \text{MVN} \left[\begin{bmatrix} Xb + Z_{ga}ga + Z_{gn}gn \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} Z_a Ga Z_a' + Z_n Gn Z_n' + R & Z_a' Ga & Z_n' Gn & R \\ Ga Z_a' & Ga & 0 & 0 \\ Gn Z_n' & 0 & Gn & 0 \\ R & 0 & 0 & R \end{bmatrix} \right]$$

Where:

y: was a vector of observation for BW and WW,

b: was a vector of fixed effects (e.g, contemporary groups, age of dam, sex, or other fixed effects, such as breed group, breed percentage or heterosis),

ga : vector of additive genetic effects of groups direct and maternal intrabreed (**A**) and interbreed (**AB**),

gn : vector of direct non-additive genetic group effects and interbreed maternal (**A/B**),

ca : vector of additive genetic effects for the direct and maternal multi-breed effects of animal **c** ,

cn : vector of direct and maternal intra-breed and in-breed non-additive genetic effects for one locus and two loci of animal **c**,

e: vectors of errors.

X : was a known incidence matrix relating fixed effects in **b** to observation in **y**,

Zga : was the incidence matrix that relates records of animals to elements of the vector **ga** through:

- 1) the probabilities of having alleles of breed **A** in the animal for direct intrabreed genetic effects,
- 2) the probabilities of having alleles of breed **A** in the mother of the animal for genetic effects intraracial maternal, 3) the probabilities of having alleles of races **A** and **B** in the parents of the animal to direct interracial genetic effects, and 4) the probabilities of having alleles of races **A** and **B** in the parents of the mother of the animal for maternal genetic effects interracial,

Zgn = was the incidence matrix that relates records of animals to elements of the vector **gn** through: 1) the probabilities of have alleles of breeds **A** and **B** at one and two loci in the animal

for direct interracial non-additive genetic effects, and 2) the probabilities of having alleles of breed **A** and **B** in one and two loci from the mother of the animal for genetic non-additives maternal interracial effects.

Za = was the incidence matrix that relates animal records to elements of the **ca** vector: 1) to the animal for direct multibreed additive genetic effects, and 2) to the animal's mother for maternal multibreed additive genetic effects,

Zn = was the incidence matrix that relates animal records to elements of the vector **cn** through 1) the probabilities of having alleles of one breed or of both breeds at one locus or at two loci of the animal for direct non-additive genetic effects, and 2) the probabilities of having alleles of one breed or both breeds at one locus or two loci in the dam of the animal for maternal non-additive genetic effects,

Ga = matrix of direct and maternal additive multibreed genetic variances and covariances among the elements of the vector **ca**. Matrix **Ga** = $(\mathbf{I} - 0.5\mathbf{P})^{-1}\mathbf{Ba}(\mathbf{I} - 0.5\mathbf{P}')^{-1}$, where **P** = lower triangular matrix that relates fathers and mothers to animals with records, **P'** = transpose of **P**, and **Ba** = diagonal matrix in block with equal elements additive genetic variances and covariances multiracial between elements of the vector **ca**. Additive multibreed genetic covariance formulas for any number of breeds are given in Lo et al. (1993) and Elzo (1994, 1995), and for two breeds in Elzo and Wakeman (1998). Additive multibreed genetic variances and covariances are linear functions of intra-breed and interracial additive variances and covariances. Variances and covariances in **Ba** are calculated with the rules specified by Elzo (1990a).

Gn = matrix of intra-breed and in-breed non-additive genetic variances and covariances between elements of vector **cn**. Matrix **Gn** = $(\mathbf{I} - 0.5\mathbf{P})^{-1}\mathbf{Bn}(\mathbf{I} - 0.5\mathbf{P}')^{-1}$, where **Bn** = block diagonal matrix with elements equal to direct and maternal intrabreed and interracial non-additive genetic

variances and covariances for one locus and two loci between elements of the vector **cn**. Elements of **Bn** can be calculated with the rules specified by Elzo (1990b).

R = block diagonal matrix of residual variances and covariances between elements of vector **e**. The blocks are of size **nt** × **nt**, where **nt** = number of characters (i.e., 2 × 2 in the case of BW and WW). Residual variances contain multi-breed environmental variances and variances due to additive and non-additive genetic effects not contained in the model. The same is true for residual covariances. Environmental variances and covariances are linear functions of intra-breed and inter-breed environmental variances and covariances.

An important modification on the multibreed model suggested by Elzo, was proposed by Pollak (2006). This multibreed animal model was a simplified version of the Arnold (1992) developed by Rodriguez-Almeida et al. (1997). The modified model was fit: random, the nonadditive components were ignored, variances were homogenous, and fixed heterosis effects were assumed the same for any breed combination. The authors also fit multiple traits (birth and weaning weights) with direct and maternal effects for both traits (Pollak, 2006). With this procedure, they were able to estimate a separate effect, obtaining direct and maternal, and breed effects in the model.

In 1997, the NBCEC consortium developed a multibreed, multi-trait evaluation for the American Simmental Association (ASA) using the procedure proposed by Rodríguez-Almeida et al. (1997), concluding that this methodology will be extended to incorporate information on the breed composition of cows and heterosis in the predictions of phenotypic performance. In addition, with this type of analysis, the contribution of the genetic merit of an animal is shown depending on the racial composition of the couple. Even so, it allows customizing the use of the EPDs for each livestock farm (Pollak, 2006).

2.7 Literature Cited

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CHAPTER 3 – HETEROSIS EFFECTS ON AGE AT FIRST CALVING IN A MULTIBREED BEEF CATTLE HERD IN PANAMA

Summary

The aim of this study was to estimate the influence of heterosis and breed percentage on age at first calving (AFC) in beef cows. Data from 619 cows and 1,142 individuals in the pedigree from the multibreed herd of the Livestock experimental station of Panama Agricultural Innovation Institute (IDIAP) in Gualaca, Panama, were used. The herd was comprised of the following genetic groups and according to their breed percentage: tropical adapted Brahman (BR), Nellore (NE), Undefined *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (OTH); crossbreeds (CX), Beefmaster (BF), Three CX(F1 x different BT), R1(Backcross BR), R2 (Backcross BT), Composites (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu). An animal model was utilized to estimate variance components for AFC. Fixed effects included in the model consisted of the contemporary group with outcross and breed percentage included as linear covariates. The contemporary group was defined by the year of calving. The average AFC was 42.7 ± 10.5 months, ranging from 18 to 69 months. The estimated regression coefficient for AFC on heterosis was -0.046 ± 0.009 month/percent of outcross ($P = 0.001$). Lower AFC was observed for the F1, R2, and B2, with 39.8 months, 39.9 months, and 39.5 months, respectively. The difference for these breeds was found to be 12.7%, 12.5%, and 13.4%, respectively, when they were compared to the Zebu group. Additionally, a reduction in AFC was also observed for the Beefmaster (-0.13 ± 0.05 months; $P = 0.029$) and the OTH breeds category

(-0.14 ± 0.04 months; $P = 0.001$). A heritability of 0.17 ± 0.10 was estimated for AFC, which classifies it as a lowly heritable trait. These results suggest that heterosis had a beneficial influence on AFC measurements in a multibreed beef cattle herd in Panama.

3.1 Introduction

Livestock in Panama occupies more than 37% of the agricultural landscape and employs more than 20% of the labor force in the rural sector. However, measures of cattle performance suggest low production efficiency, which is reflected mainly in low reproductive ability. Specific to beef cattle in Panama, an average annual calving rate of 54% is reported, with estimates ranging from 35% to 60% (INEC, 2020). Improvement in reproductive performance has been suggested to be up to 4 times more economically important than the final product or carcass value (Melton, 1995). Even with the economic importance of reproduction, beef cattle breeding programs in Panama have focused mainly on improving carcass and growth traits and not reproductive rates.

Given the tropical climate conditions in Panama, Zebu cattle are the most predominant breeds in cow-calf systems. In Panama, Zebu represents approximately 80% of the cattle population. Additionally, crossbreeding systems have been widely used to capture the value of heterosis in growth and reproductive traits. Heterosis was defined by Dickerson (1973) as the difference in phenotype between the mean of the F1 crossbred offspring and the mean of their purebred parents. In animal breeding, this advantage is usually expressed as mid-parent heterosis or the superiority of the F1 cross over the mean performance of both parents. Furthermore, the greater the compositional differences between the parent breeds, the greater the effect of heterosis, especially for low heritability traits (Schiermister et al., 2015). Reproductive traits have been reported in the literature to have low heritability ($h^2 < 0.20$), however, given the high economic

impact of reproductive ability on the livestock production system, it becomes an attractive target for genetic improvement programs (Formigoni et al., 2005). Therefore, the biggest challenge for breeders in Panama is to improve the reproductive performance of a beef herd by producing sexually precocious females with higher fertility rates and longevity to improve economic efficiency (Campos et al., 2014; Pravia et al., 2014; Simões et al., 2020).

Collecting, measuring, and evaluating fertility traits in tropical conditions is difficult as beef cattle are raised in extensive pastures (Cavani et al., 2015). One economically relevant reproductive trait that indicates a herd's fertility is the age at first calving (AFC). This trait is related to puberty and is easily measured (Boligon et al. 2010; Berry and Evans, 2014; Costa et al., 2019). The Zebu beef breeds are considered non-precocious, given that their age at puberty has been reported to vary from 22 to 36 months, with a corresponding range in AFC of 34 to 45 months (Dias et al. 2003; Azevedo et al. 2006). A genetic improvement program focused on reducing the age at first calving for beef herds in Panama would reduce the costs associated with raising replacement heifers and ultimately help to reduce costs associated with beef production (Cavani et al., 2015), and in the case of crossbreeding systems, taking advantage of heterosis is one of the most effective strategies to help improve these traits (Boligon et al. 2010). Therefore, the objectives of this study were to determine heterosis and breed percentage effects on age at first calving in a multibreed beef cattle herd in Panama.

3.2 Materials and Methods

The data used in this study were obtained from an existing database; therefore, the study was not subject to animal care and use committee approval.

3.2.1 Data collection and description

The data used in the current study were provided by the Livestock Experimental Station of Panama Agricultural Innovation Institute (IDIAP) in Gualaca, Panama, which is in the province of Chiriqui. This experimental station is located in a Tropical Premontane wet forest life zone (Holdridge, 1971), with an average elevation of 100 m, 4,200 mm of annual rainfall, and an average daily temperature of 26° C and 80% relative humidity. With a clay loam soil, with a pH of 4.6, low organic matter (5.0%), low in phosphorus (1.0 ug/ml), medium in potassium (50 ug/ml), low in calcium (0.09 meq/100ml), and magnesium (0.03 meq/100ml), and high in aluminum (1.1 meq/100ml). The predominant type of pasture is *Brachiaria humidicola* CIAT 679, managed in a rotational system of 7 days of grazing and 35 days of rest and not fertilized.

The data were generated between the years 2000 to 2020 and included 619 heifers with records for AFC and 1,140 individuals in a 3-generation pedigree built from the individuals with AFC observations. Heifers were bred via artificial insemination and/or natural service after 18 months of age or when their body weights were greater than 318 kg. Calving seasons were concentrated in the April to June and October to December periods, which corresponded to wet season for the region. The herd was comprised of the following genetic groups and breed percentages: tropically adapted Brahman (BR), Nellore (NE), undefined *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and an other category (OTH). Specific breed crosses in the data consisted of crossbreeds (*Bos Indicus* x *Bos taurus* cross in different percentages) (CX), Beefmaster (BM), Three CX (F1 x different BT), R1(Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5%

Zebu). Calving year, calving season, calving age, and calf sex were recorded for all animals. Individual outcross was calculated using the breed percentages of the individual's parents using the formula presented by Bourdon (2000), shown below.

$$\text{Degree of outcross} = [1 - \sum_{i=1}^n P_{s_i} P_{d_i}] * 100 \quad (\text{Eq3.1})$$

Above, P_{s_i} was the proportion of the i^{th} breed in the sire and P_{d_i} was the proportion of the i^{th} breed in the dam of the individual.

3.2.2 Genetic Evaluation for Age at First Calving

Age at first calving was evaluated using a single trait animal model to estimate the influence of heterosis, breed, and additive genetic effects on AFC. This model is presented below in matrix form.

$$y = Xb + Zu + e \quad (\text{Eq.3.2})$$

In the above equation, y was a vector of AFC observations, b was a vector of unknown fixed effects (consisting of year, breed group, and breed percentage or degree of outcross as covariate, utilized in three different analyses), u was a vector of unknown direct additive genetic effects, X and Z were known incidence matrices relating observations in y to both fixed and random effects in b and u , respectively and e was a vector of unknown residual errors. The expected value of y was assumed to be Xb , and variances were assumed to be:

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

Above, **A** represented Wright's numerator relationship matrix, **I** was an identity matrix whose order is equal to the number of observations in **y**, and σ_a^2 and σ_e^2 were the additive genetic and residual variances, respectively. All analyses were performed using the statistical software package ASREML 3.0 (Gilmour et al., 2009).

3.3 Results and Discussion

3.3.1 Descriptive Statistics

The average AFC measurement in these data was 42.7 ± 10.5 months, ranging from 18 to 69 months. The distribution of AFC has shown in **Figure 1**, it is evidence of no specific calving season in this population. Summary statistics for AFC according to breed group are presented in **Table 3.1**. Considerable differences in the number of records per breed group were observed, as Zebu was the largest group representing approximately 37.1% of the data. The next largest group was the F1 representing 18.5% of the data, and the Three CX breed definition representing 18.0% of the data. The *Bos taurus* influenced groups Composite, R1, R2, Upgrade, B₁, Japanese, Creole, and B₂ groups comprised 10.1%, 7.9%, 3.06%, 1.61%, 1.61%, 0.6%, 0.5%, and 0.3% of the data, respectively.

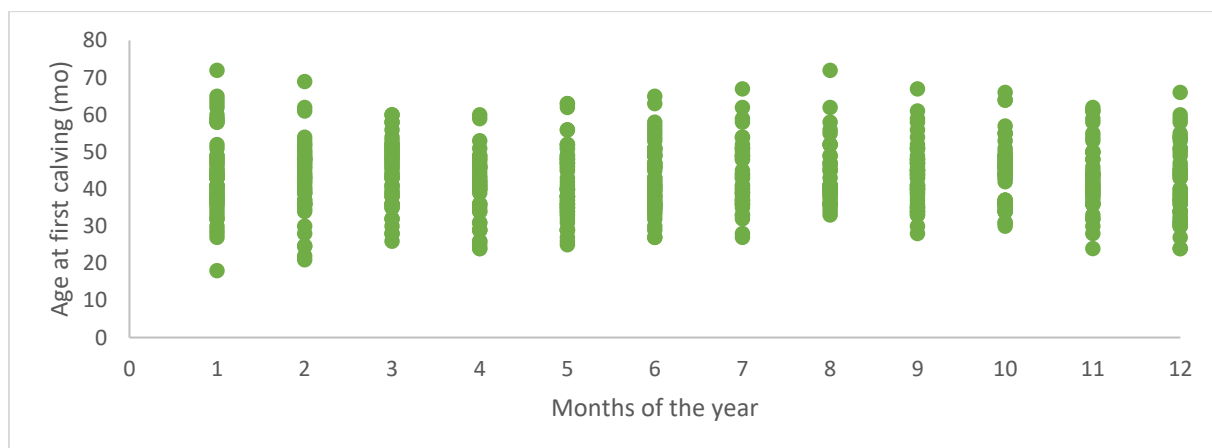


Figure 3.1. Distribution of age at first calving through the months of the year in a multibreed herd in Panama

Table 3.1. Summary statistics for age at first calving according to breed group in a multibreed herd in Panama.

Breed group	N	Average	SD	Min.	Max.
Zebu	230	45.6	8.1	24.0	67.0
F1	115	39.8	8.7	24.0	69.0
Three cx	112	41.1	8.7	18.0	63.0
Composite	63	44.1	11.8	21.0	67.0
R1	49	44.6	7.3	27.0	58.0
R2	19	39.5	11.0	26.0	60.0
Up grade	10	44.8	10.0	34.0	63.0
B1	10	44.1	7.7	29.0	55.0
Japanese	4	43.0	19.4	26.0	64.0
Creole	3	44.0	5.2	38.0	47.0
B2	2	39.5	14.8	29.0	50.0
Total	619	42.7	10.5	18.0	69.0

Zebu (Brahman, Nellore, Undefined Zebu), F1 (Zebu x *Bos taurus*), Three cx (F1 x different *Bos taurus*), R1 (Backcross Brahman), R2 (Backcross *Bos taurus*), Composite (combination of at least 4 different breeds with a Zebu percentage less than 25%), Upgrade (87.5% Brahman 12.5 *Bos taurus*), B1 (62.5% Zebu + 37.5% *Bos taurus*), Japanese (Wagyu), Creole (Guymí Panamanian Creole), B2 (62.5% *Bos taurus*+ 37.5% Zebu).

This data structure reflected the commercial beef herds used in Panama. It represents one of the challenges associated with using field data for multibreed analyses, as acknowledged in previous reports by Golden et al. (2009). In this study, the authors stated that multibreed data for analyses can be confounding and can drive confusion, especially in establishing differences between the breed additive direct effects, additive maternal effects, heterosis effects, and contemporary group effects. However, according to Giess (2022), data from commercial populations provide the greatest opportunity for the collection of rare and meaningful information useful for the genetic improvement of seedstock cattle. The average degree of outcross observed in this study was 54.65 (ranging from 0 to 100), and its effects, as well as those relative to breed differences on AFC measurements, are presented in **Table 3.2**. The average degree of outcross or heterosis found in

this population suggests that the averages performance expected should be the equivalent to 54.65% of the F1 performance which corresponds to 100% of heterosis.

Table 3.2. Average degree of outcross (heterosis) for age at first calving, in a multibreed herd in Panama.

N	Expected Heterosis (%)
234	0
11	25
71	50
12	75
291	100
Total:619	Average: 54.65

3.3.2 Analysis of Variance

Breed group effects presented as a deviation from the Zebu breed group are shown in **Table 3.3**. These results indicate that the Zebu breed group had the oldest AFC among all breeds in the data, which is in agreement with the findings from Magaña (2001), who reported a reduction of five months in AFC for F1 (Brown Swiss x Zebu) heifers and between two or three months for heifers with 25% to 75% of Brown Swiss composition. In this study, the F1, R2, and B2 had a lower average of AFC with 39.8 months, 39.9 months, and 39.5 months (**Table 3.1**), respectively, which represents a 12.7%, 12.5%, and 13.4% improvement when they were compared to Zebu group ($P = 0.001$).

Table 3.3. Estimate best linear unbiased estimate (BLUE), and standard errors for age at first calving according to breed group in a multibreed herd in Panama.

Breed group	Average	SE
Zebu	0.00	0.00
F1	-4.849	1.098
Three cx	-5.478	1.153
Composite	-3.185	1.449
R1	-1.811	1.370
R2	-8.464	2.273
Up grade	-3.533	3.082
B1	-1.880	2.802
Japanese	-0.1089	4.361
Creole	1.650	4.945
B2	-8.659	6.097

Zebu (Brahman, Nellore, Undefined Zebu), F1 (Zebu x *Bos taurus*), Three cx (F1 x different *Bos taurus*), R1 (Backcross Brahman), R2 (Backcross *Bos taurus*), Composite (combination of at least 4 different breeds with a Zebu percentage less than 25%), Upgrade (87.5% Brahman 12.5 *Bos taurus*), B1 (62.5% Zebu + 37.5% *Bos taurus*), Japanese (Wagyu), Creole (Guymí Panamanian Creole), B2 (62.5% *Bos taurus*+ 37.5% Zebu).

Breed percentage effects on AFC are presented in **Table 3.4**. These results indicate the greatest reduction in AFC is realized for both the Beefmaster (-0.13 ± 0.05 months; $P = 0.029$) and OTHER (-0.14 ± 0.04 months; $P = 0.001$). In a similar study described by Vargas and Elzo (2009) in Colombia, the greatest reduction in AFC was for the Zebu x Angus cross (-281.2 ± 41.9 d; $P < 0.001$). These authors stated that Zebu genetics involved in adaptability may have helped the expression of *Bos taurus* precocity genes. Under tropical conditions, crossbreeding programs focused on taking advantage of the early maturity and complementarity of *Bos taurus* x *Bos indicus* beef cattle have a high economic impact on the cow-calf system when compared to *Bos indicus* females (Núñez- Domínguez et al., 1991).

Table 3.4. Estimated values ($\pm$ SE) in months, and significance level of the linear covariates included in the model according breed percentage in a multibreed beef cattle herd in Panama.

Effect	Estimate for Age at First Calving	P-value
Brahman (%)	0.07 ± 0.009	0.001
Nellore (%)	-0.038 ± 0.11	0.787
Undefine Zebu (%)	-0.039 ± 0.029	0.238
Beefmaster (%)	-0.1363 ± 0.05	0.029
Wagyu (%)	-0.04 ± 0.026	0.549
Charolais (%)	-0.013 ± 0.029	0.341
Simmental (%)	-0.1051 ± 0.029	0.009
Angus (%)	-0.1076 ± 0.068	0.412
Guaymi (%)	-0.016 ± 0.04	0.944
Red Angus (%)	-0.068 ± 0.029	0.110
Romosinuano (%)	0.03 ± 0.13	0.780
Limousin (%)	-0.017 ± 0.061	0.723
Senepol (%)	-0.052 ± 0.038	0.441
Others (%)	-0.1465 ± 0.04	0.001

The estimated regression coefficient for AFC on heterosis was -0.046 ± 0.009 month/percent of outcross ($P = 0.001$) (**Table 3.5**). This heterosis effect was similar to that reported by Vergara and Elzo (2009), who found a negative but non-significant estimate for the effect of heterosis on AFC (-26.0 ± 21.0 d; $P = 0.18$). In that regard, both Syrstad (1985) and Restle et al. (1999) reported negative estimates for heterosis effects ranging between -8 to -12% in *Bos indicus*-*Bos taurus* crosses. Furthermore, heterotic effects of crossbred individuals are known to depend upon the differences in allele frequencies of the loci contributing to variation in the trait, so the larger these differences, the greater the benefit from heterozygosity (Kumar et al., 2018). These findings are relevant since, in the present study, we show an older AFC average for females with a higher Zebu breed percentage.

Table 3.5. Component of variance, Wald F statistics, significance, heterosis regression estimate, and heritability for age at first calving in a multibreed herd in Panama.

Effect	Estimate	P-value
Year	429.39	0.001
Heterosis (%)	-0.046±0.009	0.001
Genetic variance	12.620 ± 7.42	-
Residual variance	58.571 ± 7.42	-
Phenotypic variance	71.190 ± 4.29	-
Heritability	0.17 ± 0.10	-

The variance components and estimates of heritability are also presented in **Table 3.5**. The AFC heritability estimate was 0.17 ± 0.10 , which is within the estimates reported by Cammack et al. (2009; 0.1 to 0.3) for breeds in the United States, Vergara and Elzo (2009; 0.15) for a multibreed population in Colombia, Talahari et al., (2003; 0.13) for the Camchim breed in Brazil, Casas and Tewolde (2001; 0.28) for Romosinuan in Costa Rica; but lower than those reported by Magaña et al. (2001) and Estrada – León et al., (2008; 0.46) in Mexico for a Brahman and a multibreed herd. The low estimate of the heritability of AFC in this study suggests the implementation of breeding programs aimed at improving the general fertility of the herd using the AFC trait is possible, and appropriate used would represent an economic benefit for the system. Also, reducing AFC may lead to a shorter first calving interval (time from first calving to 2nd calving) because these heifers will have enough time to recover their body condition and resume estrous quickly under optimal management and nutritional conditions (Mercadante et al., 2000). Under tropical environmental conditions, Santana et al. (2013), suggested that mass selection for puberty in Nelore females has the potential to increase the proportion of heifers that reach puberty at an age between 12 to 15 months, and that would support first calving at two years of age.

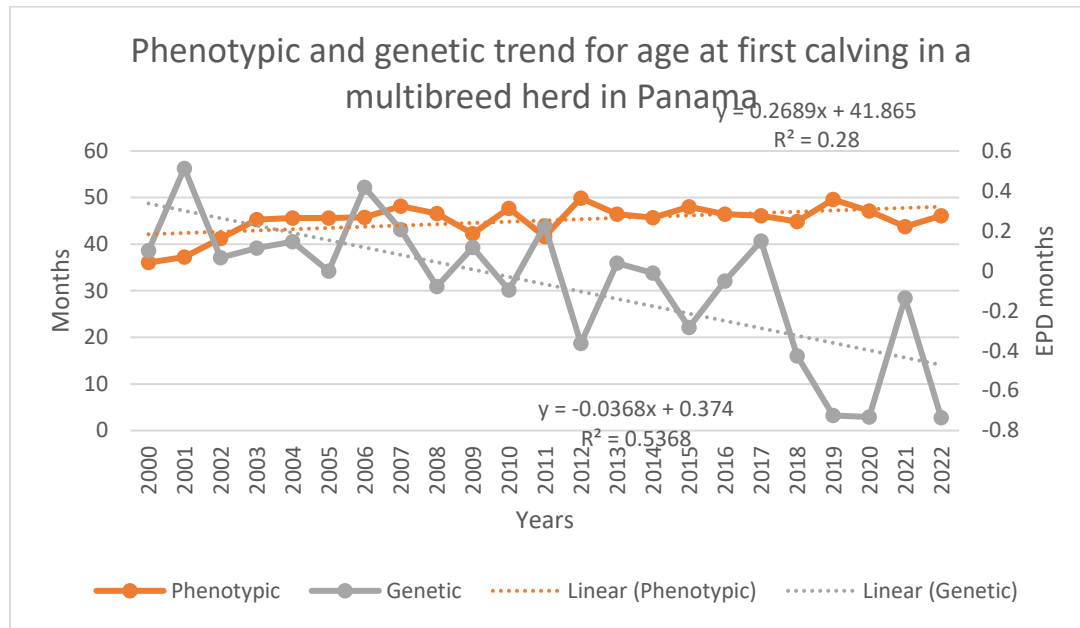


Figure 3.2. Phenotypic and genetic trend for age at first calving in a multibreed herd in Panama

The genetic and phenotypic trends are shown in **Figure 3.2**. Regardless of the increasing phenotypic trend for AFC, a negative genetic trend was observed. The contradictory slope of the phenotypic and genetic trends is evidence of the influence of the environment on reproductive traits. The above statement suggests that implementing a management strategy for a heifer's development that can allow the expression of the genetic potential, can contribute to the reduction of AFC. Those strategies can include the strategic use of forage and /or providing some energetic and protein supplements when it is needed. In this regards, González-Stagnaro et al. (2007), and Castillo-Badilla et al. (2019), reported a reduction on age at first service and AFC for Brahman, *Bos Indicus* * *Bos taurus*, and dairy heifers, implementing an improved management system that combined pasture management and strategic energetic and protein supplementation. According to

Roberts et al. (2009), rate of growth pre-weaning and early post weaning has a large influence on reproductive success in the first breeding and will be determinant in the AFC.

In Brazil, Michale et al. (2013), concluded that if an aggressive program of nutritional and hormonal intervention were to be used in Nelore and Nelore & Angus crossbred heifers, acceptable pregnancy rates in heifers bred to AI at 12 to 15 months of age and therefore age at first calving at 2 years old would be realized. The decreasing genetic trend for AFC began in 2005. This coincides with a major introduction of *Bos taurus* breeds in this population. This introduction caused the composition of the herd population to change, increasing the proportion of *Bos taurus* genetics in the crossbred cattle, consequently lowering the predictions for AFC over time. But as mentioned above, environmental factors have an important effect on reproductive performance and can prevent the expression of genetics (Vergara et al., 2009). In this case, the management, pasture, nutrition, and health protocols remained essentially the same during this period; and they could be a limitation for these cows from achieving shorter AFC.

3.4 Conclusion

In this study, a beneficial effect of heterosis in AFC was observed, with a reduction of up to 5 months in the F1 (100% heterosis) individuals when compared to the Zebu breed. The best AFC averages were for the F1, R2, Three CX, and B2 breed groups. Based on the results obtained, the breeds that have percentages of *Bos taurus* between 50% and 75% presented the best AFC averages. Regardless of the low heritability estimate found in this multi-breed population, implementing a selection strategy will generate positive and sustainable responses in the long term if sufficient data is reported so as to implement a genetic improvement program. In this population, there was evidence of an upward trend in AFC from the use of Zebu cattle, the group with the highest average AFC (45.9 months), but a larger-scale study is required to obtain conclusive data

in this regard. The opposite trajectory between the phenotype for age at first calving and the estimated genetic potential in this population suggests adjusting the environment (management, nutrition, health, etc.) to achieve a lower AFC.

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CHAPTER 4 – HETEROSIS EFFECTS ON CALVING INTERVAL AND GESTATION LENGTH IN A MULTIBREED BEEF CATTLE HERD IN PANAMA

Summary

The aim of this study was to estimate the influence of heterosis and breed percentage on calving interval (CI) and gestation length (GL), and the correlation between age at first calving (AFC) and CI. Data included 1,291 repeated observations of CI and GL from 502 cows with a 3-generation pedigree consisting of 2,840 individuals, from the multibreed herd of the livestock experimental station of the Panama Agricultural Innovation Institute (IDIAP) in Gualaca, Panama. The herd was comprised of the following genetic groups and according to their breed percentage: tropical adapted Brahman (BR), Nellore (NE), Undefined *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (OTH). Additionally, various crosses amongst these breed groups were evaluated and consisted of crossbreeds (CX), Beefmaster (BM), Three CX (F_1 x different BT), R1 (Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu). The Zebu influenced breed group represented 50.03% of this population, followed by the F_1 , the Three CX, composites, and R1, representing 22%, 13.89%, 6.11%, and 5.34%, respectively. The other breed groups represented less than 2.5% of the population. A repeated records animal model was utilized to estimate variance components for both CI and GL. A bivariate animal model was used to estimate the genetic correlation between CI and AFC. Fixed effects for all models consisted of contemporary group, age of dam, calf sex,

degree of outcross, and breed percentage. Contemporary group was defined by calving year. The average CI was 572.6 ± 140 days, with a range of 315 to 910 days, and for GL the average was 284.2 ± 6.3 days, with a range of 272 to 298 days. The regression of CI and GL on heterosis was not significant ($P > 0.05$). A lower CI was observed for the F1, and Three CX, translating to 558.7 days and 567.2 days, which represents 2.3% and 1.3% reduction in CI, respectively, when compared to the Zebu group. Calving interval was estimated to be lowly heritable (0.037 ± 0.026), however, a positive genetic trend over the duration of the study. The analysis between CI and AFC revealed a moderate genetic correlation (0.49 ± 0.36) which allows the establishment of a selection program to improve AFC and CI, due to the pleotropic effect, which would improve the fertility of this multibreed herd in Panama.

4.1 Introduction

Calving interval is the period between successive parturitions, and is closely related to the yearly production cycle, which influences the amount of milk a cow produces, and is probably the best indicator of a cow's reproductive efficiency (Mukasa-Mugerwa, 1989; Pryce et al., 2004). The reproductive efficiency of a herd is one of the main components of a cattle farm's economic and productive performance. Calving interval estimates in Zebu cattle have been reported in the literature to range between 12.2 to 26.6 months (Mukassa-Mugrewa, 1989; Gebrekidan et al., 2012), and with an older AFC, the Zebu breed is reproductively inefficient when compared to other breeds of cattle.

Another strategy to improve the efficiency of beef production is the use of crossbreeding (Perotto et al. 2001). With crossbreeding, it is possible to introduce desirable genes in the target populations, changing existing genotypic frequencies (Su et al., 2009; Clasen et al., 2018). Rege

(1998) indicated that the effect of heterosis can result in an average gain of 11% for age at first calving (AFC) and of 9% for calving interval (CI) over the average of the parent breeds.

Calving interval comprises the number of days open from parturition to conception and the gestation length of the cow, which can be influenced by seasonal nutritional conditions, year, parity, season of calving, environmental stress, and disease (Assemu and Dilip, 2014). Calving interval is a fertility trait that can be used in selection programs to minimize the negative effects of selection for production on fertility (Mostert et al., 2010). In seasonally breeding herds, the aim is to achieve conception by 75 to 85 days post-parturition, depending on breed, so that calving intervals are maintained at 365 days. Additionally, reasonably short calving intervals of 12-13 months indicate an optimum combination of good management and a sound physiological condition of the cow (Belay Zeleke, 2014).

From a physiological point of view, the resumption of ovarian cyclicity is largely dependent on luteinizing hormone (LH) pulse frequency. Both dairy and beef cows have an early resumption of follicular growth within 7 to 10 days postpartum. The fate of the dominant follicle within the first follicular wave is dependent on the LH pulse pattern (Crowe et al., 2014). In beef cows, a prolonged interval to resumption of ovulation is associated with suckling and maternal bond effect inhibiting ovulation. However, energy balance changes, body condition score at calving, dry matter intake, and health disorders can also affect the resumption of cyclicity (Crowe et al., 2014; Shallo et al., 2014).

In Panama, the reproductive performance of cattle is poor. The indicators show that the age at first calving is greater than 36 months (Gonzalez - Murray et al., 2021), and the calving rate per year is lower than 60% (INEC, 2020). These statistics have resulted in many farmers looking for alternatives to improve production, one of which is the introduction of exotic breeds (such as

Angus, Simmental, Wagyu, Charolais and others) for both milk and meat production, hoping to obtain better productive and reproductive parameters. A highly developed practice in cattle production systems in a tropical environment is the introduction of specialized breeds through crossbreeding. This strategy is favored today to increase meat production systems' productivity, profitability, efficiency, and sustainability (Vargas et al., 2000).

The challenge for farmers in Latin American countries is to identify those animals that achieve maximum productive performance in a given agro-ecological environment (Elzo y Borjas 2004; Martínez et al., 2008), and maintain a balance between longevity and generation intervals to obtain the greatest genetic gain per unit of time (Perotto et al. 2006). As the calf is largely the sole output in beef cow enterprises, reproductive efficiency is a key determinant of profitability, irrespective of the system of production employed; however, to improve the efficiency of calf production in Panama, it is important to evaluate the breeds groups and heterosis effect through productivity indicators to know the relative performance of the breeds and crosses of Zebu and *Bos taurus* cattle in the cow–calf system. Therefore, the objective of this study was to determine heterosis and breed percentage effects on calving interval and gestation length in a multi-breed beef cattle herd in Panama.

4.2 Materials and Methods

The data used in this study were obtained from an existing database; therefore, the study was not subject to animal care and use committee approval.

4.2.1 Data Collection and Description

The data were provided by the Livestock Experimental Station of IDIAP in Gualaca, which is in the Chiriqui province in Republic of Panama. The data were generated between the years

2000 to 2021. This experimental station is located in a Tropical Premontane wet forest life zone (Holdridge, 1971) with an average elevation of 100 m above sea level, 4,200 mm of annual rainfall, and an average daily temperature of 26° C and 80% relative humidity. With a clay loam soil, with a pH of 4.6, low organic matter (5.0%), low in phosphorus (1.0 ug/ml), medium in potassium (50 ug/ml), low in calcium (0.09 meq/100ml), and magnesium (0.03 meq/100ml), and high in aluminum (1.1 meq/100ml). The predominant type of pasture is *Brachiaria humidicola* CIAT 679, managed in a rotational system of 7 days of grazing and 35 days of rest and not fertilized.

Data included 1,291 repeated records from 502 cows with both CI and GL observations. The 3-generation pedigree consisted of 2,840 individuals, including 147 unique sires. Cows were bred via artificial insemination (AI) and/or natural service 60 days post-calving. From replicate records, GL observations were assigned to females based on the service method (AI or Bull). The phenotype for CI was calculated as the period between two consecutive calving. Cows that never calved or were used in embryo transfer programs were not included in this database. Calving seasons were concentrated between April and June as well as October and December; however, they were spread throughout the year and grouped into two seasons: the dry season from January to April and the rainy season from May to December. The herd was comprised of the following genetic groups according to their breed percentage: tropically adapted Brahman (BR), Nellore (NE), undefined *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (Oth); crossbreeds (CX), Beefmaster (BF), Three cx (F1 x different BT), R1 (Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu). Calving year, calving season, calving age, sex of calf, and age of dam

were recorded for all animals and included as systematic fixed effects in the analysis. Individual outcross was calculated using the breed percentages of the individual's parents and the formula presented by Gregory et al., (1994) and Bourdon (2000), shown below (Eq.4.1).

$$\text{Degree of outcross} = [1 - \sum_{i=1}^n P_{s_i} P_{d_i}] * 100 \quad (\text{Eq.4.1})$$

In the above equation, P_{s_i} was the proportion of the i^{th} breed in the sire and P_{d_i} was the proportion of the i^{th} breed in the dam of the individual.

4.2.2 Genetic evaluation for calving interval

Calving interval and calving length were evaluated using a repeated records animal model to estimate the effect of heterosis and breed percentage (Eq.4.2). This model equation is presented below in matrix form.

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_p\mathbf{p} + \mathbf{e} \quad (\text{Eq.4.2})$$

In the above equation, $\mathbf{y}$ was a vector of CI or GL observations; $\mathbf{b}$ was a vector of unknown fixed effects consisting of year (as contemporary group), breed group, calf sex, calving season, and breed percentage or degree of outcross (heterosis) as a linear covariate, $\mathbf{a}$ was a vector of unknown direct additive genetic effects, $\mathbf{p}$ was a vector for unknown permanent environmental effects, and $\mathbf{e}$ was a vector of unknown residual errors. The matrix $\mathbf{X}$ was a known incidence matrix relating observations in $\mathbf{y}$ to fixed effects in $\mathbf{b}$, $\mathbf{Z}_a$ was the incidence matrix for relating observations in $\mathbf{y}$ to the random additive genetic effects in $\mathbf{a}$, $\mathbf{Z}_p$ was an incidence matrix relating observations in $\mathbf{y}$ to the permanent environmental effects in $\mathbf{p}$.

The random effects were assumed to have means of zero and variances shown below:

$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & I_p\sigma_{pe}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & I_e\sigma_e^2 \end{bmatrix} = \begin{bmatrix} G & \mathbf{0} \\ \mathbf{0} & R \end{bmatrix}$$

Above, $\mathbf{A}$ represented Wright's numerator relationship matrix. $\mathbf{I}_p$ was an identity matrix whose order was equal to the number of animals with repeated records, $\mathbf{I}_e$ was an identity matrix whose order was equal to the number of observations, and σ_a^2 , σ_{pe}^2 and σ_e^2 were the additive genetic, permanent environment and residual variances, respectively. The model shows that those permanent environmental effects for different animals are uncorrelated, and within an animal, there was no correlation between its additive and its permanent environmental effect. The total phenotypic variance was the sum of the three variance components (Quaas, 1984).

All analyses were performed using the statistical software package ASREML 3.0 (Gilmour et al., 2009).

The mixed model equations for a model with repeated records look like:

$$\begin{bmatrix} X'X & X'Z_a & X'Z_p \\ Z_a'X & Z_a'Z_a + \lambda A^{-1} & Z_a'Z_p \\ Z_p'X & Z_p'Z_a & Z_p'Z_p + \gamma I \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{a} \\ \mathbf{pe} \end{bmatrix} = \begin{bmatrix} X'y \\ Z_a'y \\ Z_p'y \end{bmatrix} \text{ where } \lambda = \sigma_e^2/\sigma_a^2 \text{ and } \gamma = \sigma_e^2/\sigma_{pe}^2$$

The phenotypic and genetic correlations between AFC and CI were estimated. Here, a bivariate animal model with repeated records was performed (Eq.4.3). This model is presented below:

$$\begin{aligned} y_1 &= Xb_1 + Z_a a_1 + e \\ y_2 &= Xb_2 + Z_a a_2 + Z_p pe_2 + e \end{aligned}$$

(Eq.4.3)

Where y_1 was a vector of AFC, y_2 was a vector of CI observations; $\mathbf{b}$ was a vector of unknown fixed effects (consisting of year, breed group, sex of the calf, calving season, and breed percentage or degree of outcross as a linear covariate), $\mathbf{a}$ was a vector of unknown direct additive genetic effects, $\mathbf{pe}$ was the vector for permanent environmental effects, and $\mathbf{e}$ was a vector of unknown residual errors. The matrix $\mathbf{X}$ was an incidence matrix relating fixed effects in $\mathbf{b}$ to observations in $\mathbf{y}$, and $\mathbf{Z}_a$ was an incidence matrix for relating observations in $\mathbf{y}$ to the random effects in $\mathbf{a}$, $\mathbf{Z}_p$ was the incidence matrix for relating observations in $\mathbf{y}$ to the permanent environmental effects in $\mathbf{p}$.

The above model variance structure is show as follows:

$$Var \begin{bmatrix} a_1 \\ a_2 \\ pe_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a1}^2 & A\sigma_{a_1a_2} & 0 & 0 & 0 \\ A\sigma_{a_2a_1} & A\sigma_{a2}^2 & 0 & 0 & 0 \\ 0 & 0 & Ipe\sigma_{pe2}^2 & 0 & 0 \\ 0 & 0 & 0 & In\sigma_{e1}^2 & In\sigma_{e1e2} \\ 0 & 0 & 0 & In\sigma_{e2e1} & In\sigma_{e2}^2 \end{bmatrix}$$

Above, $\mathbf{A}$ represented Wright's numerator relationship matrix, $\mathbf{I}_p$ was an identity matrix whose order was equal the number of animals with repeated records, $\mathbf{I}_n$ was an identity matrix whose order was equal to the number of observations and σ_a^2 , σ_{pe}^2 and σ_e^2 were the additive genetic, permanent environment and residual variances, respectively, and $\sigma_{a_1a_2}$ and σ_{e1e2} represented the genetic and residual covariances between AFC and CI. The permanent environmental effects for different animals were assumed to be uncorrelated, and within an animal, there was no correlation between its additive and its permanent environmental effect. The total phenotypic variance was the sum of the three variance components (additive, permanent environment, and residual).

4.3 Results and Discussion

4.3.1 Descriptive Statistics

The average values for CI and GL are shown in Table 4.1. All the breeds groups have average CI above the range suggested as optimal for beef cattle (365 d – 396 d) (Keoatile et al. 2009). This CI represents a 63% calving rate per year on average for this population. The largest CI was observed in B1, Upgrade, and Japanese groups with $664.2 \text{ d} \pm 89.2 \text{ d}$, $634.4 \text{ d} \pm 186.0 \text{ d}$, and $630.0 \text{ d} \pm 117.1 \text{ d}$ respectively. For all the breeds groups, the average GL was $284.2 \text{ d} \pm 6.3 \text{ d}$, this is within the expected normal range (265 d to 295 d), reported by Wheat et al., (1958), Mornan, et al. (2009).

The Zebu breed group represents 50.03% of this population, followed by the F1, Three CX, composites, and R1, representing 22%, 13.89%, 6.11%, and 5.34%, of the observations respectively. The other breed groups were less than 2.5%, where R2, Upgrade, and B1, represents 0.69%, each one and the Japanese and B2 were 0.3%, and 0.23% respectively.

Table 4.1. Summary statistics for calving interval and gestation length for breed group, in a multibreed herd beef cattle in Panama.

Breed group	N	Average Calving Interval	SD	Min	Max	Average Gestation length	SD	Min	Max
Zebu	646	574.8	141.7	315	910	287.9	7.6	272	298
F1	286	558.7	139.5	315	907	285.1	5.1	272	298
Three cx	179	567.5	133.1	318	903	286.3	7.3	274	298
Composite	79	598.8	145.1	334	876	285.9	8.0	272	298
R1	69	571.6	150.7	352	908	286.9	8.6	272	298
R2	9	569.8	141.2	350	772	289.1	10.2	274	298
Upgrade	8	634.4	186.0	417	857	288.2	10.0	272	298
B1	8	664.2	89.2	509	790	285.1	6.9	276	296
Japanese	4	630.0	117.1	510	787	283.5	4.7	277	287
B2	3	574.3	119.4	467	703	287.3	8.5	279	296
Total	1291	572.6	140.9	315	910	284.2	6.3	272	298

Zebu (BR, Ne, BI), F₁ (Zebu x BT), Three cx (F₁ x different BT), R₁ (Backcross BR), R₂ (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B₁ (62.5% Zebu + 37.5% BT), Japanese (Wagyu), Creole (Guymi Panamanian Creole), B₂ (62.5% BT + 37.5% Zebu).

The calculated outcross distribution is shown in **Table 4.2**. In these data, the largest number of individuals were calculated with 100% heterosis representing the F₁ individuals followed by individuals with 0% heterosis, representing straight-bred groups. The average heterosis in this population was 61.25%. This heterosis percentage was similar to the reported by Gama et al., (2002) for the Montana crossbreeding system in Brazil of (0.637±0.384). Montana crossbred is a composite with the ability to perform well in tropical climates, made up of 37.5 % adapted breed (Nellore, Senepol, or Bosmara), and up to 87.5% Bos taurus (Continental, Adapted Bos taurus, and British type breeds).

Table 4.2. Average degree of outcross (heterosis) for calving interval and gestation length, in a multibreed herd in Panama.

N	Expected Heterosis (%)
360	0
36	25
187	50
1	68.5
47	75
2	87.5
14	93.5
7	93.75
631	100
Total:1291	Average: 61.25

4.3.2 Analysis of variance

Breed group was not found to be a significant source of variation of CI ($P = 0.161$). However, taking the Zebu group as a reference, we found negative estimates for heterosis of CI for the F1, Three CX, R1, and R2 (**Table 4.3**), evidencing the positive effect of *Bos indicus* x *Bos taurus* crossbreeding system. This was in agreement with Freitas et al. (1980) and Perotto et al. (2006), who reported a reduction in CI (ranging between 8% to 12%) for different *Bos Indicus* x *Bos taurus* breed crosses. This study found a greater heterosis effect for The F1 and Three CX, with 2.3% and 1.3%, respectively. Non-significant differences were observed for calf sex and seasonality effects ($P > 0.05$) on CI; however, a higher average was found for male calves and dry season (**Table 4.3**). GL varied significantly by AOD ($P < 0.001$), where two- and three-year-old dams show the lowest average GL with 279.3 ± 9.2 and 279.8 ± 7.2 days, respectively; all other systematic fixed effects in the models had no statistically significant influence ($P > 0.05$) (**Table 4.5**).

Table 4.3. Estimate best linear unbiased estimates (BLUE) for calving interval according to breed group, in a multibreed herd in Panama.

Item	Average	SE
Zebu	0.00	0.00
F1	-25.66	11.17
Three cx	-26.17	13.16
Composite	5.14	18.27
R1	-20.68	18.50
R2	-14.25	47.63
Up grade	45.45	49.62
B1	55.73	50.34
Japanese	48.00	72.17
B2	46.72	82.20
Male	43.69	56.71
Female	37.92	56.73
Dry season	0.00	0.00
Rainy season	-1.977	8.397

Zebu (Brahman, Nellore, Undefined Zebu), F1 (Zebu x *Bos taurus*), Three cx (F1 x different *Bos taurus*), R1 (Backcross Brahman), R2 (Backcross *Bos taurus*), Composite (combination of at least 4 different breed with a Zebu percentage less than 25%), Upgrade (87.5% Brahman 12.5 *Bos taurus*), B1 (62.5% Zebu + 37.5% *Bos taurus*), Japanese (Wagyu), Creole (Guymí Panamanian Creole), B2 (62.5% *Bos taurus*+ 37.5% Zebu).

Non-significant statistical differences were observed for breed percentage on CI ($P > 0.05$), (Table 4.4). This result was similar to the finding of Riley et al. (2010), who reported no differences ($P > 0.05$) when comparing the reciprocal Brahman – Romosinuano and Brahman – Angus crossbreds for CI. Wald F statistics and significance are presented in Table 4.5. Year and AOD were significant sources of variation for CI ($P < 0.001$) (Table 4.5). A trend for a decreasing CI was observed up to 12 years of age (Figure 4.1). Similar trends were reported by Perotto et al. (2006), and Damiran et al. (2018) where older cows had shorter CI regardless of the breed composition.

Table 4.4. Estimated values ($\pm$ SE) in days, and significance level for calving interval of the linear covariates included in the model according breed percentage in a multibreed beef cattle herd in Panama.

Effect	Estimate for Calving Interval	P-value
Brahman (%)	-0.2409 $\pm$ 0.81	0.230
Nellore (%)	0.1722 $\pm$ 1.22	0.373
Undefine Zebu (%)	-0.3395 $\pm$ 0.83	0.896
Beefmaster (%)	-0.6675 $\pm$ 1.52	0.705
Wagyu (%)	-1.237 $\pm$ 0.86	0.549
Charolais (%)	-0.5370 $\pm$ 0.86	0.569
Simmental (%)	-0.6943 $\pm$ 0.87	0.929
Angus (%)	-1.363 $\pm$ 1.16	0.402
Guaymi (%)	-0.4878 $\pm$ 1.25	0.991
Red Angus (%)	-0.6369 $\pm$ 0.85	0.759
Romosinuano (%)	0.6429 $\pm$ 0.13	0.406
Limousin (%)	-0.3570 $\pm$ 1.11	0.607
Senepol (%)	-0.6670 $\pm$ 0.89	0.071
Others (%)	-0.5671 $\pm$ 0.98	0.561

Table 4.5. Wald F statistics and significance for calving interval and gestation length in a multibreed herd in Panama.

Effect	Calving Interval		Gestation Length	
	Estimate	P-value	Estimate	P-value
Year	4.65	0.0001	3.22	0.0001
Age of dam	1141.72	0.0001	1200000	0.0001
Season	0.01	0.926	1.92	0.168
Calf Sex	0.54	0.585	0.20	0.941

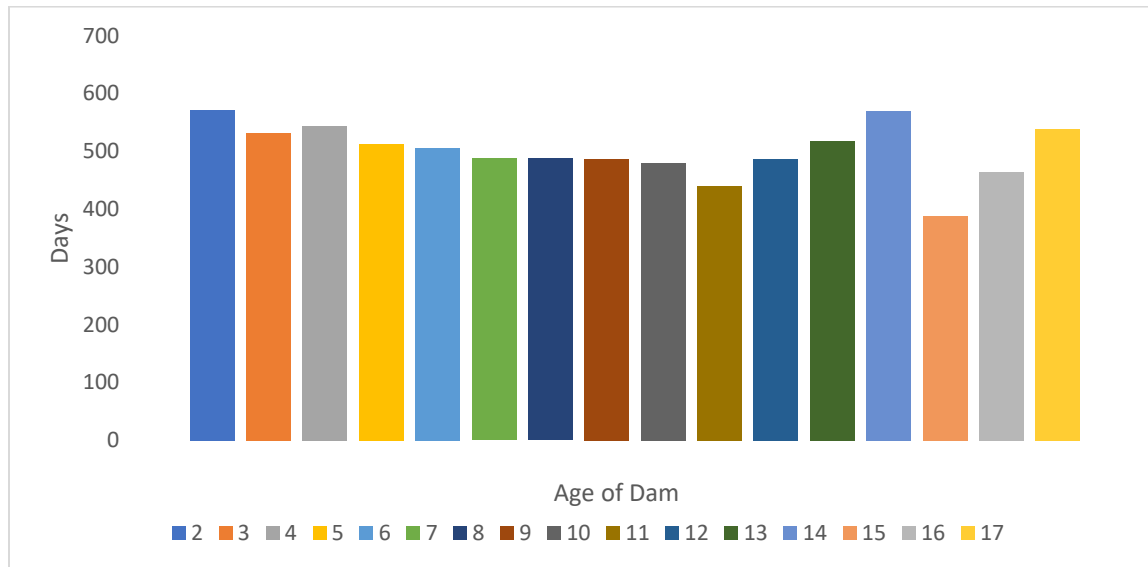


Figure 4.1. Average calving interval according to the age of dam in a multibreed herd in Panama.

The genetics components and heterosis regression are presented in Table 4.6. The estimated regression coefficient for CI on heterosis was -0.1140 ± 0.1017 days/percent of outcross ($P = 0.266$) (**Table 4.6**). This heterosis effect was similar to the report of Gama et al., (2022), who found negative estimates of heterosis for CI (-12.7 d; $P = 0.001$). In this study the average reduction in days on CI -11.40 d which represent 1.99% heterosis. In this regard, Syrstad (1985), Rege (1998), Penasa et al. (2010), Vieira et al. (2022), and Gama et al. (2022) reported a negative heterosis estimate in days ranging between -12 d to -30 d. In general, heterotic effects of crossbred individuals shows a desirable direction of reducing the calving interval, increasing the herds efficiency Vieira et al., (2022).

A non- significant effect of heterosis on GL was found (-0.009752 d $\pm$ 0.05213 d), ($P > 0.05$), (**Table 4.6**). This was in agreement with Touchberry et al., (1966), Sagebiel et al., (1973), and Reynolds et al., (1980) that reported a no heterosis effect on GL ($P > 0.05$), but they found a reduction trend that range between -0.5 d to -1.6 d. Calf sex effect was non-significant (**Table**

4.5), however, male sex estimate was $2.157 \text{ d} \pm 3.671 \text{ d}$, and female estimate was $1.896 \text{ d} \pm 3.673 \text{ d}$, over the population mean for GL. These estimates were similar to the estimate reported by Reynolds et al. (1980) where dams calving male calves tend to have a larger gestation length.

Table 4.6. Heterosis regression coefficient, variance components and heritability for calving interval and gestation length, in a multibreed herd in Panama.

Item	Calving Interval	Gestation Length
Heterosis (%)	-0.1140 ± 0.1017	-0.009752 ± 0.05213
Genetic variance	695.69 ± 484.42	$0.000022559 \pm 0.0000013319$
Permanent environment variance	0.052299 ± 0.0024357	1.1773 ± 1.4729
Residual variance	17779.0 ± 828.03	37.873 ± 2.26
Phenotypic variance	18475.0 ± 740.39	39.050 ± 1.8324
Heritability	0.037 ± 0.026	0.0 ± 0.0

The variance components emphasize the high influence of environmental effect on these reproductive traits. CI heritability was 0.037 ± 0.026 , (**Table 4.6**). This heritability was similar to the values reported by Mostert et al. (2010), and Faraji et al. (2011), ranging between 0.011 and 0.069 and lower than the estimate reported by Vergara et al., 2009 (0.11 ± 0.06).

The low heritability for CI means that this trait is highly influenced by the environment, being nutritional status one of the most influential factors; affecting the hormonal balance required to initiate the resumption of the estrous cycle after parturition (Diskin et al., 2016). According to Hess et al. (2005), if prepartum and postpartum nutrient intake is inadequate, a longer postpartum anestrus interval will be evidenced, and consequently a longer CI will be observed. Could there also be a heat stress response in fertility?

Nutrient intake is reflected in Body Condition Score (BCS). Increasing feed intake promotes fat storage, which may be a prerequisite for restoring ovarian function in postpartum

cows. An increased in BCS is required for the resumption of estrous cycles in nutritionally induced anestrus cows (Richards et al., 1989). In this regard, Hess et al. (2005), reported a high and negative correlation between BCS at calving and CI ($r = -0.75$) and also with BCS change postpartum the correlation was ($r = -0.43$; $P < 0.001$).

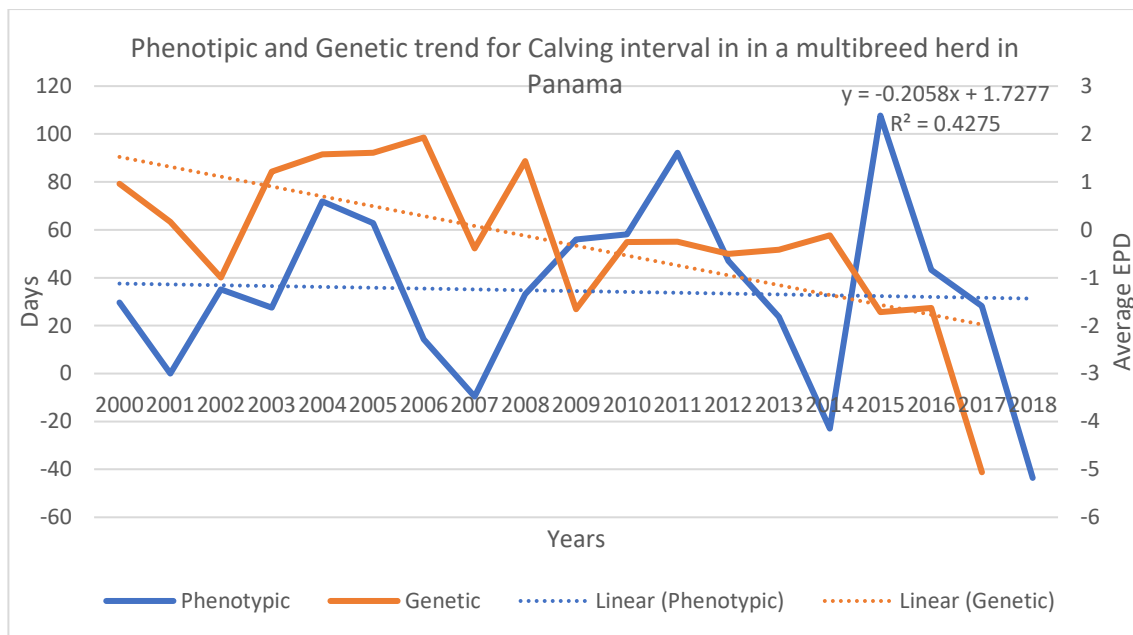


Figure 4.2. Phenotypic and genetic trends for calving interval in a multibreed herd in Panama.

The genetic and phenotypic trends are shown in the **Figure 4.2**. Regardless of the high environmental influence observed in CI, a favorable genetic trend was observed. The estimated EPD's regressed on year of birth shows a reduction of -0.2058 days per year; however, this genetic gain per unit of time is masked by the environmental effect, evidenced in the phenotype's tendency. A similar trend was reported by Mackinnon et al. (1989) in a multi-breed evaluation in Australia and attributed this to different environmental effects which highlights the changes in body

condition, the effects of season on the availability of nutrients, and heat stress. In addition, Rudder et al. (1985) and Richards et al. (1986) stated that other factors that affect cattle fertility in tropical and subtropical conditions are the physiological status and stress caused by parasites.

Table 4.7. Components of variance, heritability, the phenotypic and genetic correlations for age at first calving and calving interval in a multibreed herd in Panama

Item	AFC	CI
σ_a^2	28.464 ± 15.554	831.10 ± 474.58
σ_e^2	47.703 ± 14.148	17656.0 ± 811.22
σ_{pe}^2	-	0.16000E-05
$\sigma_{a1,a2}$	76.089	-
$\sigma_{e1,e2}$	-4.0281	-
σ_p^2	152.26 ± 55.679	18487.0 ± 742.31
$\sigma_{p1,p2}$	72.060	-
h^2	0.18 ± 0.11	0.04 ± 0.02
$r_{g(AFC.CI)}$	0.49 ± 0.36	-
$r_{p(AFC.CI)}$	0.043 ± 0.047	-

σ_a^2 additive genetic variance, σ_e^2 residual variance, σ_{pe}^2 permanent environment variance, σ_p^2 , phenotypic variance, $\sigma_{a1,a2}$ genetic covariance, $\sigma_{e1,e2}$ residual covariance, $\sigma_{p1,p2}$ phenotypic covariance, h^2 heritability, $r_{g(AFC.CI)}$ genetic correlation, $r_{p(AFC.CI)}$ phenotypic correlation.

A moderate genetic correlation between AFC and CI was evidenced in this evaluation (0.4947) (**Table 4.7**). This means that cows that calve at an early age will also have a shorter calving interval. According to Perotto et al. (2006), this can highly influence the efficiency and the economy of the herds, due to a reduction in fixed costs and production cycles, increasing profitability.

Based on the evidence of the present study, it is necessary to improve the management conditions to achieve the maximum expression of the genetic potential related to fertility in this population.

4.4. Conclusion

A beneficial effect of heterosis on CI (-0.114 days/percentages of heterosis) were observed in this study, however, no effect was evidenced on GL. The F1 and Three cx group shows the lowers CI. The breed effect evidenced that increasing the percentage of Romosinuano and Nellore negatively influenced the calving interval. Despite not observing a phenotypic tendency to decrease CI, an improvement in EPD was evident over the years, which is a clear effect of the high influence of environmental factors on the phenotype. A low heritability for CI (0.037), was estimated for this population. However, the estimated median genetic correlation between AFC and IC (0.49), allows the establishment of a selection program on AFC, with its subsequent decrease in CI; which would improve the fertility of the herd in the medium and long term.

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CHAPTER 5 – HETEROSIS EFFECTS ON PRE-WEANING TRAITS IN A MULTIBREED BEEF CATTLE HERD IN PANAMA

Summary

The aim of this study was to estimate the influence of heterosis and breed percentage on birth weight (BW) and weaning weight (WW) in beef cows in a tropical environment. Data from 900 calves and 2,843 individuals in the pedigree from the multibreed herd of the Panama Agricultural Innovation Institute (IDIAP) in Gualaca, Panama, were used. The herd was comprised of the following genetic groups and according to their breed percentage: tropically adapted Brahman (BR), Nellore (NE), Un define *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (OTH); crossbreeds (CX), Beefmaster (BM), Three CX (F1 x different BT), R1(Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu). A bivariate animal model for BW and WW was utilized to estimate variance components. Contemporary group was defined as the year of birth. The effects of sex, birth season, weaning season, and age of dam were included as categorical fixed effects. Weaning age, degree of outcross, and breed percentage were included as linear covariates, and individuals as the random effects. The estimated regression coefficient for BW on heterosis was not significant (-0.04 ± 0.06 ; $P > 0.05$), and for WW was 0.072 ± 0.027 kg ($P < 0.05$). Lower BW and WW were observed for the Japanese, and B1, while R2 and Upgrade had the highest average WW ($P < 0.05$). Heritability for BW was found to be low (0.14 ± 0.06) and moderate for WW (0.26 ± 0.09). The proportion of variation of WW accounted by the maternal permanent environment for WW was (0.2 ± 0.09). The estimated genetic correlation

between additive genetic BW and WW was 0.63 ± 0.30 , while a negative, additive genetic correlation was observed for WW direct and WW maternal (-0.43 ± 0.37). These results suggested that heterosis had a beneficial influence on WW but a limited effect on BW. Additionally, increasing the percentage of WA and BR negatively influenced WW measurements in these data.

5.1 Introduction

In Panama, Zebu cattle (*Bos indicus*) is the most predominant breed in cow-calf systems due to the tropical environmental conditions. *Bos indicus* cattle show greater resistance to internal and external parasites and greater tolerance to elevated ambient temperatures and humidity when compared to *Bos taurus* beef breeds (Hansen, 2004). However, different breeds have been introduced to the country and are widely used in crossbreeding systems to obtain the benefits of heterosis in growth and reproductive traits. The beneficial effects of crossbreeding on animal performance have been well established (Dickerson, 1973; Gregory and Cundiff, 1980. Weaber and Spangler, 2013), benefiting lowly heritable traits such as those related to reproduction, and contributing to improving other traits such as the maternal ability in females (Bourdon, 2000). The reproductive efficiency of a herd is one of the main components of a cow-calf system's economic and productive performance (Prayaga et al., 2009; Berry et al., 2014; Cooke et al., 2020). Other important traits that affect the system efficiency are the preweaning traits: birth weight (BW) and weaning weight (WW). According to Theunissen et al. (2013), many beef producers derive their income from the total weight of weaned calves. This income can be maximized if optimum cow numbers are matched with the correct genetic potential in the appropriate production environment (Correa et al., 2006; Burrow, 2012). According to Bourdon (2000), the growth of an animal is influenced by genetic and non-genetic factors, and in the tropics, reduced growth is the main limiting factor, among other factors, such as reproduction (Jones and Hennessy, 2000).

In the cow-calf system, preweaning traits are a combination of a direct genetic effect, a maternal genetic effect, a maternal permanent environment effect (for most preweaning traits), and temporary environmental effects (Bijma, 2006; Mrode, 2014; Schaeffer, 2019). All these factors need to be accounted for in a genetic evaluation (Falconer and Mackay, 1996). Muraio et al. (2008) stated that the physiological and physical capacities of a dam and its uterine environment have influences on the fetus and calf as maternal ability; furthermore, the milking ability of a dam is a key factor influencing preweaning traits.

Considerable variation exists among breeds of beef cattle that are an important genetic resource for use in crossbreeding to exploit complementarity and heterosis. Heterosis enables crossbred dams to increase milk production and thus provides a maternal environment that supports greater preweaning growth (Dickerson, 1973; Gregory and Cundiff, 1980; Leal et al., 2018; Bonifazi et al., 2021). According to Michael et al. (2022), knowledge of the genetic effects of breeds and their crosses in various climatic and forage conditions can be used to identify optimal breed combinations and crossbreeding systems for existing markets.

Evaluating all breeds of cattle and combinations among them in all environments is difficult; for this reason, the challenge, especially in tropical zones, is to identify those animals that achieve maximum productive performance in a given agro-ecological environment (Vergara, 2014). In tropical environments, reduced performance is the major limiting factor in the cattle production system (Jones and Hennessy 2000); due to the great challenge of expressing a high genetic potential in those environmental conditions (Duarte Ortuno et al. 1988; Howden et al. 1999). Based on the heterogeneity of herds in tropical regions due to the introduction of multiple breeds and the different crossbreeding systems utilized, it is necessary to carry out a multi-breed evaluation that includes all crossbred and purebred individuals into a single analysis that accounts

for the direct and maternal breed and heterosis effects (Arnold et al., 1992; Elzo, 1992, Cardoso & Templeman, 2004; Pollak, 2006; Gamma et al., 2022).

Given the above statements, the aim of this study was to estimate the influence of heterosis and breed percentage on birth weight (BW) and weaning weight (WW) in a multi-breed cattle herd in Panama, as well as estimate direct and maternal genetic components of birth weight (BW) and weaning weight (WW).

5.2 Materials and Methods

The data used in this study were obtained from an existing database; therefore, the study was not subject to animal care and use committee approval.

5.2.1 Data Collection and Description

The data were provided by the Livestock Experimental Station of IDIAP in the Gualaca, province of the Chiriqui Republic of Panama. Data were generated between the years 2000 to 2021. This experimental station is located in a Tropical Premontane wet forest life zone (Holdridge, 1971), with an average elevation of 100 m above sea level, 4,200 mm of annual rainfall, and an average daily temperature of 26° C and 80% relative humidity. With a clay loam soil, with a pH of 4.6, low organic matter (5.0%), low in phosphorus (1.0 ug/ml), medium in potassium (50 ug/ml), low in calcium (0.09 meq/100ml), and magnesium (0.03 meq/100ml), and high in aluminum (1.1 meq/100ml). The predominant type of pasture is *Brachiaria humidicola* CIAT 679, managed in a rotational system of 7 days of grazing and 35 days of rest and not fertilized.

Data included 2,006 BW and 900 WW records in addition to 2,840 individuals included in a 3-generation pedigree. Birth weight was recorded within 24 hours of birth, and WW was recorded between 6 and 9 months of age.

Calving seasons were concentrated between April to June and October to December; however, they were spread throughout the year and grouped into two seasons: the dry season from January to April and the rainy season from May to December. The herd was comprised of the following genetic groups and according to their breed percentage: tropically adapted Brahman (BR), Nellore (Ne), Un define *Bos indicus* (BI), Guaymi Creole (CR), Senepol (SP) Romosinuano (RS); *Bos taurus* (BT), Simmental (SM), Angus (AN), Red Angus (AR), Limousin (LM), Charolais (CH), Wagyu (WA), and Others (Oth); crossbreeds (CX), Beefmaster (BF), Three CX (F1 x different BT), R1(Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), B2 (62.5% BT + 37.5% Zebu) (**Table 5.1**). This diverse composition is a typical representation that can be found in herds of beef cattle in Panama. Birth year, birth season, weaning age, weaning season, sex of calf, and age of dam were recorded. The degree of outcross for all animals was also calculated and included as a systematic fixed effect in the analysis. Individual outcross was calculated using the breed percentages of the individual's parents (**Table 5.2**) and the formula presented by Bourdon (2000); Gregory et al (1994), shown below (Eq.5.1).

$$\text{Degree of outcross} = \left[1 - \sum_{i=1}^n P_{s_i} P_{d_i} \right] * 100$$

(Eq.5.1)

In the above equation, P_{s_i} was the proportion of the i^{th} breed in the sire and P_{d_i} was the proportion of the i^{th} breed in the dam of the individual.

5.2.2 Genetic evaluation for birth weight and weaning weight

A two-trait animal model was used to estimate the effect of heterosis and breed percentage on BW, and WW(Eq.5.2). This model is presented below, in matrix form; where the subscripts ₁ and ₂, reference "trait 1" and "trait 2", respectively. The models for each trait were specified as follows:

$$\begin{aligned} \mathbf{y}_1 &= \mathbf{X}_1 \mathbf{b}_1 + \mathbf{Z}_{a_1} \mathbf{a}_1 + \mathbf{e}_1 \\ \mathbf{y}_2 &= \mathbf{X}_2 \mathbf{b}_2 + \mathbf{Z}_{a_2} \mathbf{a}_2 + \mathbf{Z}_{m_2} \mathbf{m}_2 + \mathbf{Z}_{p_2} \mathbf{pe}_2 + \mathbf{e}_2 \end{aligned}$$

(Eq. 5.2)

where $\mathbf{y}$ represented a vector of observations for i^{th} trait (1= BW, 2 = WW), $\mathbf{b}$ corresponded to a vector for fixed effects (consisting of birth year, breed group, calves sex, birth season, weaning season, age of dam (as categorical), and weaning age, breed percentage or degree of outcross as a linear covariate, according to the model) that included the contemporary groups for the i^{th} trait, $\mathbf{a}$ was a vector containing the random direct additive genetic effects for the i^{th} trait, $\mathbf{m}_2$ was a vector containing the animal random maternal genetic effects for the WW, $\mathbf{pe}_2$ was a vector containing the animal permanent random environmental effects for the WW; $\mathbf{e}$ was a vector of random residual effects for the i^{th} trait. $\mathbf{X}$ was the incidence matrices that relate observations in $\mathbf{y}$ to levels of fixed effects in $\mathbf{b}$ and $\mathbf{Z}_{a_1}$ was the incidence matrices that relate observations in $\mathbf{y}$ to levels of random animal genetic effects in $\mathbf{a}$, for BW, $\mathbf{Z}_{a_2}$ was the incidence matrices that relate observations in $\mathbf{y}$ to levels of random animal genetic effects in $\mathbf{a}$, for WW, $\mathbf{Z}_{m_2}$ was the incidence matrices that relate observations in $\mathbf{y}$ to levels of random animal maternal genetic effects in $\mathbf{m}$, and

Z_{p_2} was the incidence matrix for relating observations in y to the permanent environmental effects in pe . In the above model variances of the random effects were assumed to be distributed as:

$$Var \begin{bmatrix} a_1 \\ a_2 \\ m_2 \\ pe_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a1}^2 & A\sigma_{a_1a_2} & A\sigma_{a_1m_2} & 0 & 0 & 0 \\ A\sigma_{a_1a_2} & A\sigma_{a2}^2 & A\sigma_{a_2m_2} & 0 & 0 & 0 \\ A\sigma_{a_1m_2} & A\sigma_{a_2m_2} & A\sigma_{m2}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & Ipe\sigma_{pe2}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & In\sigma_{e1}^2 & E\sigma_{e1e2} \\ 0 & 0 & 0 & 0 & \sigma_{e2e1}E' & In\sigma_{e2}^2 \end{bmatrix}$$

Above, A represented Wright's numerator relationship matrix, I_p was an identity matrix whose order is equal to $k \times 1$ where k is the number of animals with repeated records I_n , was an identity matrix whose order is equal to $n \times 1$ where n represent each individual animal in the estimation and σ_a^2 , σ_{pe}^2 and σ_e^2 are the additive genetic, permanent environment and residual variances, respectively and, $\sigma_{a_1a_2}$ represent the genetic covariance between BW and WW; $\sigma_{a_1m_2}$ represent the genetic covariance between BW genetic and WW maternal genetic, $\sigma_{a_2m_2}$ represent the genetic covariance between WW and WW maternal genetic; σ_{e1e2} represent the residual covariance between BW genetic and WW. The matrix E contained all zeros, except for locations corresponding to particular dams with calves in both environments, in which case that element of E was unity. The permanent environmental effects for different animals are uncorrelated, and within an animal, there was no correlation between its additive and its permanent environmental effects. The total phenotypic variance was the sum of the three variance components. The phenotypic and genetic correlation was estimated for BW and WW, as well as the correlation of direct and maternal genetic effects for WW.

5.3 Results and Discussion

5.3.1 Descriptive Statistics

Summary statistics for BW and WW are shown in **Table 5.1**. Lighter BWs were observed for the Japanese breed group with $27.5 \text{ kg} \pm 4.1 \text{ kg}$, while the Upgrade group reported the heavier BW with $35.6 \text{ kg} \pm 6.6 \text{ kg}$. The heaviest WW was observed for the R2, Upgrade, Three CX, and B2 groups with $180.0 \text{ kg} \pm 32.8 \text{ kg}$, $175.6 \text{ kg} \pm 30.9 \text{ kg}$, $171.8 \text{ kg} \pm 29.0 \text{ kg}$, and $171.6 \pm 29.3 \text{ kg}$, respectively (**Table 5.1**). These values for BW and WW are in concordance with other studies of multibreed populations in tropical or subtropical conditions, with a reported range for BW between 27.0 kg to 38.1 kg and for WW between 144.0kg to 230.7 kg, (Olson et al., 1993; Franke et al., 2001; Naser et al., 2012; Riley et al., 2014; Vergara et al., 2014; Mpofu et al., 2016; Leal et al., 2018).

The Zebu breed group represents 30.66% of this population, followed by the Three CX, composite, F1, and R1, representing 24.6%, 15.19%, 10.53%, and 7.0% of the population, respectively. The other breed groups were less than 12%, where R2, Upgrade, and B1 represent 3.49%, 2.75%, and 4.10% each, and the Japanese and B2 were 0.6% and 1.0%, respectively.

Table 5.1. Summary statistics of birth weight and weaning weight for breed group in a multibreed herd of beef cattle in Panama.

Breed group	N	Birth weight	SD	Min	Max	Weaning weight	SD	Min	Max
Zebu	658	34.5	6.3	22.0	53.0	163.1	30.6	100.2	281.0
F1	226	33.4	5.4	21.8	51.0	168.2	23.3	114.0	218.0
Three cx	528	33.6	5.1	16.8	49.0	171.6	29.3	100.7	259.0
Composite	326	34.8	6.9	19.5	52.0	164.3	28.9	100.3	239.0
R1	151	34.6	6.7	22.3	51.0	171.7	31.8	110.9	249.0
R2	75	34.0	4.1	26.0	44.0	180.6	32.8	118.8	239.6
Upgrade	59	35.6	6.6	18.6	52.0	175.6	30.9	130.0	255.0
B1	88	33.2	5.9	22.5	48.0	158.6	25.0	112.5	215.0
Japanese	13	27.5	4.1	22.5	38.0	125.5	21.4	110.0	187.0
B2	22	34.9	6.8	23.	45.0	171.8	29.0	112.1	193.3
Total	2,146	34.16	6.0	16.8	53.0	167.36	29.6	100.2	281.0

Zebu (BR, Ne, BI), F1 (Zebu x BT), Three cx (F1 x different BT), R1 (Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B1 (62.5% Zebu + 37.5% BT), Japanese (Wagyu), Creole (Guymi Panamanian Creole), B₂ (62.5% BT + 37.5% Zebu).

The calculated heterosis distribution is shown in **Table 5.2**, with the largest number of individuals with 100% followed by individuals expecting 50% of outcross. The average heterosis was 69.83% ranged from 0 % to 100%. This heterosis percentage was similar to that reported by Vergara et al. (2014) and Ferraz et al. (2022) for a multi-breed population in Colombia and for the Montana crossbreeding system (a composite with the ability to perform well in tropical climates, build up 37.5 % adapted breed (Nellore, Senepol or Bosmara), however 87.5% *Bos taurus* (Continental, Adapted *Bos taurus* and British type breeds) in Brazil, with 0.53 and 0.637 ± 0.384, respectively.

Table 5.2. The average degree of outcross (heterosis) for birth weight and weaning weight in a multibreed herd in Panama.

N	Expected Heterosis (%)
309	0
128	25
391	50
21	68.5
145	75
5	87.5
16	93.5
47	93.75
1,086	100
Total: 2,148	Average: 69.83

5.3.2 Analysis of Variance

The breed group effect was significant ($P = 0.001$). The best linear unbiased estimate (BLUE) for all the groups, seasons, and calf sex are presented in **Table 5.3**. A lower BLUE for BW and WW was found for the Japanese group, and the highest for WW was found for the R2 and Upgrade groups. Both groups, however, were similar to the Three CX (**Table 5.3**). These results are similar to those reported by Vergara et al. (2014), who found a lower BW BLUE for *Bos taurus* breeds when compared to *Bos indicus* breeds. However, Vergara et al. (2009), when conducting a similar study in the lower tropics of Colombia, found WW results that demonstrate a positive effect for the *Bos Indicus* Zebu groups (14.71 ± 4.52 kg.; $P = 0.001$) and negative for the *Bos taurus*, Angus (-24 ± 4.61 kg; $P = 0.69$), and Blanco Orejinegro (-39 ± 4.74 kg, $P = 0.21$). In another analysis of a multibreed population in the south of Colombia, Martinez et al (2012) reported a positive BLUE effect of the Zebu group, and *Bos taurus* beef group, for WW; but a negative *Bos taurus* effect when dairy breeds were included in the *Bos taurus* group. In the present study, a non-significant effect was found for birth season ($P = 0.491$); however, weaning season significantly influences the WW ($P = 0.047$), showing the rainy season a difference of 3.8 kg when

we compare it to dry season (**Table 5.3**). A seasonal difference was reported by Mpofu et al. (2016) in South Africa; but in this study, the Nguni and crossbred calves weaned during the dry season were heavier (2.59 kg, $P<0.05$) when compared to the calves that were weaned during the rainy season, regardless of breed.

Table 5.3. Best Linear Unbiased Estimate ($\pm$ SE) in kilograms, according to breed group, season, and calf sex in a multibreed beef cattle herd in Panama.

Breed group	Birth weight	SE	Weaning weight	SE
Zebu	0.25	0.59	-9.84	2.63
F1	-0.28	0.72	-5.20	3.15
Three cx	0.00	0.00	0.00	0.00
Composite	1.73	0.65	-4.99	2.89
R1	0.83	0.78	0.53	3.32
R2	-0.39	1.16	2.46	4.94
Upgrade	2.17	1.27	2.77	5.55
B1	-0.05	1.02	-12.49	4.51
Japanese	-6.57	4.09	-37.49	17.85
B2	0.74	1.79	-6.51	7.64
Season				
Rainy	-0.22	0.44	0.00	0.00
Dry	0.00	0.00	-3.80	2.01
Sex				
Male	-2.51	0.39	8.76	1.68
Female	0.00	0.00	0.00	0.00

Zebu (BR, Ne, BI), F1 (Zebu x BT), Three cx (F1 x different BT), R1 (Backcross BR), R2 (Backcross BT), Composite (combination of at least 4 different breeds with less than 25% of Zebu), Upgrade (87.5% BR 12.5% BT), B₁ (62.5% Zebu + 37.5% BT), Japanese (Wagyu), Creole (Guymi Panamanian Creole), B₂ (62.5% BT + 37.5% Zebu).

The effect of calf sex effect was significant. In this study, male calves averaged lighter BW (-2.5 ± 0.39 kg., $P= 0.001$) and higher WW (8.7 ± 1.7 , $P= 0.001$) when compared to their female counterparts (**Table 5.3**). A positive estimate for weaning age was evidenced (0.28 ± 0.03 kb., $P= 0.001$) however, the effect of breed percentage on WW presented a negative estimate for Wagyu and Brahman breed percentage with -0.05 ± 0.02 kg, and -0.13 ± 0.1 kg, ($P<0.05$) respectively.

Regressions of breed percentage on (WW or BW or Both) showed a positive but non-significant trend ($P>0.05$) (**Table 5.4**). In this regard, Franke et al. (2001), in a multi-breed study, found a similar response for the percentage of Brahman breed (-0.01 ± 5.8 kg) on WW. However, many other studies conducted in either a tropical or sub-tropical environment found a positive relationship between Brahman and Zebu breed percentages for WW (Olson et al., 1993; Vergara et al., 2009; Riley et al., 2014; Martinez et al., 2015). In the current study, all the breeds studied show a negative estimate in relation to BW ($P<0.05$), except for the Romosinuano, which shows a positive estimated 0.05 ± 0.07 ($P>0.05$) (**Table 5.4**).

No significant effect was found ($P=0.054$), for the influence of age of dam (AOD) on BW; however, for WW a significant effect was evidence ($P= 0.001$). A positive influence was observed for the AOD on WW. This positive effect comprises the age range between 4 to 12 years old (**Figure 5.1**). The maximum effect of AOD on WW was found among seven and eight years old dams. This result was in agreement with of Minyard et al. (1965), who reported that eight years was the maximum production age for cows, and within the range reported by McCormick et al., (1956), Gregory et al. (1978), Elzo et al (1987), BIF (2002), Rumpf and Van Vleck (2004), who stated that the maximum production in beef cows is between six to ten years old, with the lowest performance for the two and three year old cows.

The heterosis effect was not significant for BW. However, the estimated heterosis regression coefficient was positive and significant for WW (0.072 ± 0.026 kg / % heterosis, $P= 0.001$) (**Table 5.4**). This effect on WW, was similar to the effect found by Gregory et al., (1991); but lower than the values found by Olson et al. (1985), Riley et al. (2014), Leal et al. (2018), and Ferraz et al. (2022), who reported values ranging from 0.038 kg/ % heterosis to 0.35 kg / % heterosis of WW per percentage of heterosis in a multi-breed analysis.

Table 5.4. Estimated slopes values ($\pm$ SE) in kilograms, and the significance level of the linear covariates included in the bivariate model according to breed percentage and degree of outcross in a multibreed beef cattle herd in Panama.

Effect	Estimate for Birth Weight	P-value	Estimate For Weaning Weight	P-value
Brahman (%)	-0.06 ± 0.038	0.674	-0.05 ± 0.02	0.001
Nellore (%)	-0.13 ± 0.05	0.049	0.28 ± 0.23	0.334
Undefine Zebu (%)	-0.08 ± 0.04	0.071	0.05 ± 0.17	0.647
Beefmaster (%)	-0.058 ± 0.04	0.770	0.15 ± 0.17	0.332
Wagyu (%)	-0.09 ± 0.04	0.016	-0.13 ± 0.1	0.009
Charolais (%)	-0.04 ± 0.03	0.149	0.19 ± 0.17	0.168
Simmental (%)	-0.05 ± 0.04	0.150	0.21 ± 0.17	0.029
Angus (%)	-0.065 ± 0.04	0.929	0.08 ± 0.21	0.752
Guaymi (%)	-0.12 ± 0.05	0.167	0.03 ± 0.24	0.747
Red Angus (%)	-0.06 ± 0.04	0.456	0.05 ± 0.17	0.785
Romosinuano (%)	0.05 ± 0.07	0.925	0.09 ± 0.6	0.800
Limousin (%)	-0.075 ± 0.04	0.454	0.03 ± 0.19	0.758
Senepol (%)	-0.06 ± 0.04	0.468	0.15 ± 0.18	0.172
Others (%)	-0.032 ± 0.02	0.092	0.06 ± 0.17	0.106
Degree of outcross (%)	-0.04 ± 0.06	0.806	0.072 ± 0.026	0.001
Weaning age	-		0.28 ± 0.03	0.001

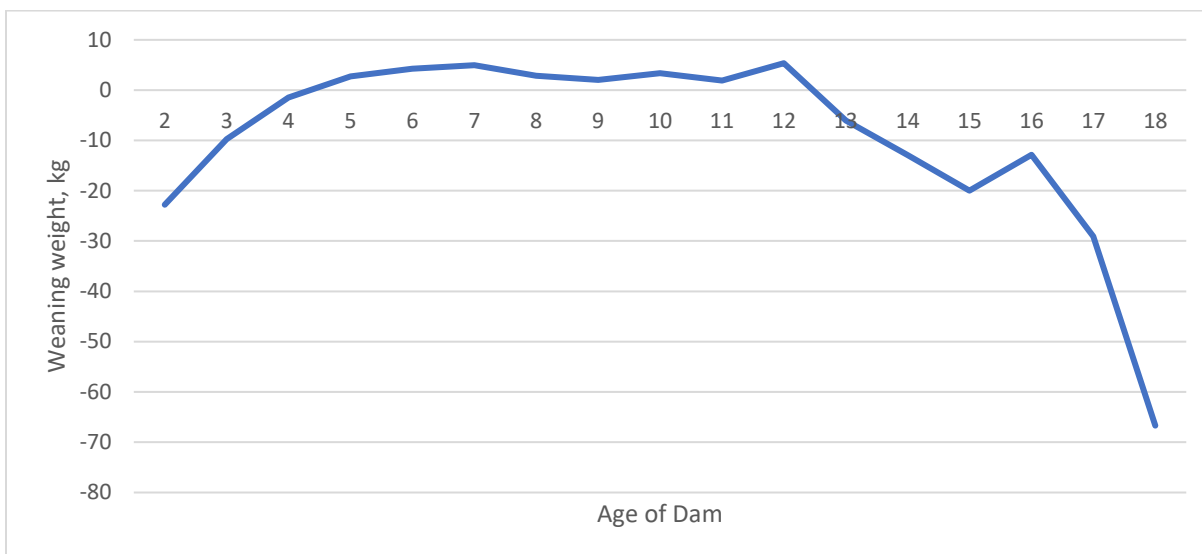


Figure 5.1. Average Best linear unbiased estimate for weaning weight according to the age of dam in a multibreed herd in Panama

The variance components for BW and WW, for direct, maternal, and permanent environments are reported in **Table 5.5**. The variance estimates obtained indicate a large influence of the environmental effect on these preweaning traits. In this study, all the different variance components were higher than the values reported by Pragaya et al. (2005), for a multibreed population in Australia but with a lower corresponding heritabilities. For BW, the heritability was estimated to be 0.14 ± 0.06 (**Table 5.5**); this heritability was lower than the values reported by Vergara et al. (2009) in Colombia, 0.24 ± 0.027 , but similar to the reported estimates by Vargas et al. (2014), in Brazil 0.12 ± 0.028 , Dominguez et al. (2003), 0.12, and Elzo et al. (1998), 0.13, for multibreed populations. Direct and maternal heritability estimates for WW were 0.26 ± 0.09 and 0.2 ± 0.09 , respectively. For the same trait, Pragaya et al. (2005) reported a direct genetic effect heritability of 0.21 ± 0.05 and 0.10 ± 0.05 for the maternal genetic effect; similar results were found by Vergara et al. (2009), where the direct and maternal heritability estimates were 0.20 ± 0.003 and 0.14 ± 0.002 respectively. In the present study, the higher direct genetic effect indicates that

the weaning weight is more influenced by the calves' own genetics for growth than by the maternal ability of the dams.

A negative genetic correlation between direct and maternal additive genetic effects was evidenced in this study for BW -0.506 ± 0.52 (**Table 5.5**); however, the large standard error encompasses zero. A similar correlation was reported by Vergara et al. (2014), -0.51 ± 0.17 , Dominguez et al. (2003), -0.97 ± 0.11 , Sarmiento et al. (2007), -0.37 ± 0.007 , for crossbreed populations in tropical environments. Similarly, a negative correlation was found between the direct and maternal effects -0.43 ± 0.37 for WW (**Table 5.5**), meaning that with the increase of maternal ability, the direct genetic effect will decrease. The estimated direct and maternal genetic correlation found in this study was similar to the value reported by Vergara et al. (2009), -0.42 ± 0.009 , but larger than the value reported by Domínguez et al. (2003), -0.37 ± 0.06 for the tropical synthetic breed Tropicarne, and with a different direction than the correlation found by Pragaya et al., (2005), 0.25 ± 0.33 , for a multibreed population. According to Baker (1980), and Robinson (1996), the estimate for genetic correlation in beef cattle can range from -0.70 estimates of genetic correlations between additive to highly positive values; however, it is more frequent to find estimates from field data with negative values. Maternal effects comprise the environment provided by the dam in the pre and postnatal stages (Albuquerque, 2001) and can affect the preweaning and early life stage performance, but in some cases, can be identified in later life performance, but in reduced levels (Mackinnon et al., 1991; Meyer, 1992). The previous statement suggests that for any early-age genetic evaluation, it is important to consider the direct and maternal genetic effect (Albuquerque, 2001).

Table 5.5. Variance component, for direct maternal and permanent environment, heritability, genetic correlation and phenotypic for birth weight and weaning weight from a bivariate model in a multibreed herd in Panama.

Effect	Birth Weight	Weaning Weight
σ_a^2	5.2915± 2.79	309.29± 112.09
σ_m^2		115.01± 119.85
σ_{am}		-142.92 ± 94.54
σ_{pe}^2		151.95± 74.85
σ_e^2	28.921±2.90	239.41± 77.16
σ_p^2	34.213± 1.83	815.66± 111.70
h_a^2	0.14± 0.06	0.26±0.09
h_m^2		0.2± 0.09
h_{pe}^2		0.1863± 0.09
r_{am}	-0.506±0.52	-0.43± 0.37
$r_{BW,WW}$	0.63± 0.30	

σ_a^2 = direct additive genetic variance; σ_m^2 = maternal genetic effect variance; σ_{am} = direct and maternal genetic effects covariance; σ_{pe}^2 = permanent environmental variance effects; σ_e^2 = residual variance; σ_p^2 = phenotypic variance; h_a^2 = direct additive heritability; h_m^2 = maternal additive heritability; h_{pe}^2 = heritability of permanent environment; r_{am} = genetic correlation between direct and maternal additive effects; $r_{BW,WW}$ = phenotypic correlation between birth weight and weaning weight.

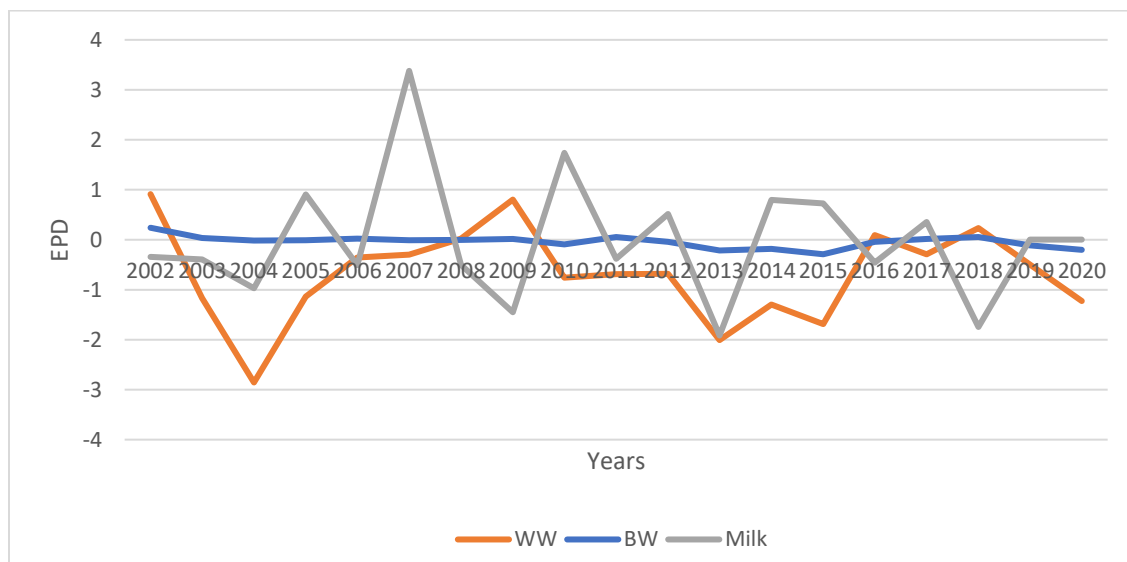


Figure 5.2. A Genetic trend for Birth weight (BW), weaning weight (WW), and Milk in a multibreed herd in Panama.

The estimation of genetic trends is a useful method to quantify the results of the selection practiced in one or multiple breeds (Cunningham and Klei, 1995). The genetic trends for BW and WW and Milk are shown in **Figure 5.2**. In this study there was a slight decrease in the BW across years; however, a nonspecific trend was found for WW and Milk, evidencing that, for this population, selection for WW or Milk production was non-evident. Bijma (2006) stated that the selection response not only depends on the change in true breeding values but also on the effect that the environment can have on the population. Based on the previous statement, we can hypothesize that the pattern observed in the genetic trend for weaning weight is a reflection of the different crossbreeding strategies used in this population, in which, due to the adverse effects of the environment on individuals with high *Bos taurus* percentage (but with greater breeding values for this trait), it is necessary to use adapted breeds, with a lower breeding value. Regardless of the nonspecific trend for WW and Milk genetics, it is possible to observe that both genetic effects have a opposite pattern each other that is expected given the negative genetic relationship.

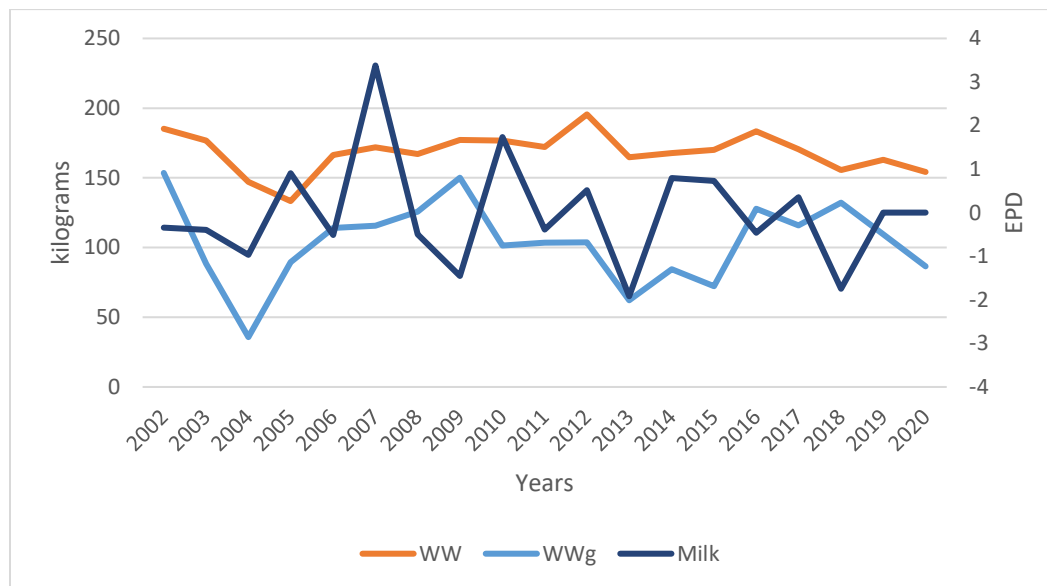


Figure 5.3. Genetic and phenotypic trends for weaning weight (WW), weaning weight direct genetic (WWg), and Milk in a multibreed herd in Panama.

The genetic and phenotypic trends are shown in **Figure 5.3**. The observed trends suggest the rate of selection for increased WW has been steady since 2006; as mentioned above, this is a reflection of a nonspecific selection criterion applied in this population. Weaning weight is an important trait in the cow–calf system because calf sales can represent 80 to 90% of annual income, and in conjunction with fertility, are fundamentals for herd productivity (Lalman et al., 2018). According to Intaratham et al. (2008), it is important to monitor annual trends for calf weights to check the validity of the predictions made and to investigate the direction of genetic change, and with this, we can verify if the selection strategies implemented are achieving the expected goals. Knowing that the primary goal of animal breeders is to maximize the rate of genetic improvement and economic benefits in a sustainable way.

5.4 Conclusion

A beneficial effect of heterosis on WW (0.072 ± 0.026 kg/percentages of heterosis) was observed in this study. However, no effect was observed for BW. A higher average of WW was found for the Three cx, R2, and Upgrade groups. The breed effect solution indicated that increasing the percentage of Wagyu and Brahman negatively influenced WW.

In the current study, a low heritability (0.14 ± 0.06) was found for BW, however, the heritability for WW was moderate (0.26 ± 0.09), with a low value for maternal genetic effects (0.2 ± 0.09). A moderate negative genetic correlation -0.43 ± 0.37 , was found between the direct and maternal genetic effect for WW, with a nonspecific genetic trend for WW and Milk EPDs, but with a steady and slightly decreasing EPD for BW. Despite not observing a defined tendency for WW EPD, it is necessary to establish an appropriate genetic selection program to improve preweaning traits and, subsequently profitability in this population in the medium and long term.

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