2024

Longevity in Afrikaner Cattle: A Survival Analysis

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LONGEVITY IN AFRIKANER CATTLE: A SURVIVAL ANALYSIS

By

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A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Animal Science

South Dakota State University

2024

THESIS ACCEPTANCE PAGE

Allison M. Bot Steffl

This thesis is approved as a creditable and independent investigation by a candidate for the master's degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ACKNOWLEDGEMENTS

I would like to thank Dr. Gonda for being my major advisor throughout my career in graduate school, for the opportunity to study at South Dakota State University, for his mentorship and friendship, and for his patience, insight and encouragement throughout the thesis writing process.

A special thank you to Dr. MacNeil and Prof. Scholtz for having the idea for this project and helping make it happen.

I would also like to extend my gratitude to Dr. MacNeil, Prof. Scholtz, and Dr. Djira for serving on my graduate committee. Thank you for the knowledge and wisdom you have shared with me during my time at SDSU.

Thank you to all of the wonderful friends that have come into my life during my time as a M.S. student. Your kindness, compassion, understanding, encouragement, and ability to bring fun into most any situation was an integral part of my success.

Thank you to my husband Nick, your constant love, forgiveness, encouragement, and support. I could not have completed this chapter without you. I am lucky to have you by my side.

To my family, thank you for always supporting me in all my adventures. Thank you for your constant love, support, encouragement, and understanding. I would not be where I am today without you.

TABLE OF CONTENTS

Chapter 2: THE EFFECT OF THE AFRIKANER INFUSION PROJECT ON LONGEVITY: A SURVIVAL ANALYSIS

Chapter 3: AFRIKANER LONGEVITY: A SURVIVAL ANALYSIS

LIST OF ABBREVIATIONS

AFC	Age at First Calving
BC1	Backcross One: F1 female x Afrikaner bull
BC2	Backcross Two: BC1 female x Afrikaner bull
EBV	Estimated Breeding Value
F1	First Crossbred Generation: Afrikaner x Bonsmara
INTERGIS	Integrated Registration and Genetic Information System
N	Number
RR	Risk Ratio

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

AFRIKANER LONGEVITY: A SURVIVAL ANALYSIS

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The Afrikaner breed of cattle is indigenous to South Africa and due to their hardiness was once the most popular breed amongst farmers. The objectives for this study were to: (1) estimate environmental effects (age at first calving, season) and (2) genetic variance affecting longevity in Afrikaner cattle using survival analysis and a Weibull model and (3) evaluate the effect of the Infusion Project on longevity utilizing a Cox model. For the first objective, age at first calving impacted longevity as younger age at first calving was associated with decreased longevity. Season of birth and year of birth also impacted longevity. For the second objective, longevity in Afrikaner cattle was lowly heritable although sufficient breeding value variation was uncovered to justify selection for this trait. For the third objective, the Infusion Project was developed to target shortcomings of the Afrikaner breed with the introgression of Bonsmara alleles into Afrikaner cattle. The first backcross generation (BC1) and the initial Afrikaner-Bonsmara cross generation (F1) had greater longevity. The second (BC2) backcross generation did not differ in longevity relative to the purebreds ($P \geq 0.05$). Infusion of Bonsmara germplasm increased longevity of the hybrid females, in the short-term.

REVIEW OF LITERATURE

Afrikaner cattle

The Afrikaner breed was once the most abundant breed of beef cattle in South Africa. Afrikaner is a Sanga type (Bos taurus africanus) breed of cattle indigenous to South Africa and is well adapted to its environment. Some adaptations include tolerance to heat and parasites, ability to reproduce in harsh conditions, and docility. The Afrikaner breed of cattle are small to medium in size with moderate maintenance requirements, minimal calving difficulties, and cow productivity. This breed is a popular choice in crossbreeding programs because of their hardiness, calving-ease, performance under natural grazing conditions, quality carcasses, and ability to produce heavy weaning crossbred calving (Scholtz et al., 2016; Khorshidi et al., 2017; Theunissen et al., 2014). In 1912, the Afrikaner Cattle Breeders' Society was founded, and was one of the first breed societies established in South Africa (Bradley and Cunningham 1999). However, the Afrikaner breed began to decline in popularity when farmers noticed slight declines in fertility and reproduction. It was initially thought that this decline may be related to increased inbreeding leading to inbreeding depression (Pienaar et al., 2018). However, the level of heterozygosity in Afrikaner cattle was found to be 0.568 using molecular markers; this level of heterozygosity suggested moderate to high variation indicating minimal inbreeding problems (Pienaar, 2015; van der Westhuizen et al., 2019).

Survival Analysis Techniques

Survival analysis is a method of statistical analysis that is utilized to analyze time-to-event or survival data (Allison 2019). Its name depends on the industry or field in which it is used: sociologists use “event history analysis” and engineers use “failure-time analysis”. Survival analysis has been applied to the medical field, health insurance, engineering, sociology, marketing, and many other types of research, including the livestock industry. Survival analysis is the most popular name for this statistical procedure and it is the name that is commonly used in the livestock industry. This method focuses on distribution of survival times during a specific stretch of time, with definitive start and end points (Katz and Hauck 1993). Cox regression is a model that is used to measure the risk of failure given a subject reaches a certain endpoint. The risk of failure is also known as the hazard rate or survival probability (Katz and Hauck, 1993). The Weibull distribution is a second method that is also used to model risk of failure (Ducrocq et al., 1998). The Cox and Weibull models are used to measure risk of failure; however, the Cox model does not make assumptions about the baseline hazard (Katz and Hauck 1993), whereas the Weibull model is a parametric (Rinne 2008). Survival analysis allows for consideration of records from subjects that are still alive at the time of evaluation (censored) as they are an important source of information along with animals that have left the herd (uncensored). Survival analysis techniques are implemented in genetic evaluation using Cox regression and the Weibull distribution (Ducrocq et al., 1998).

One difference between time-to-event data and other types of continuous data is that the time-to-event is not always observed on all subjects (Machin et al., 2006). This type of data utilizes censorship. Censorship occurs when a subject has not experienced the specified event by the end point (Katz and Hauck 1993). Survival analysis is used to explain how or why survival occurs (Allison 2019). An example of a case where survival analysis would be used is to analyze the time a cancer survivor lives after the cancer has been surgically removed. In this example, the beginning event is the cancer removal surgery, and the end event would be death. The time between the surgery and death would be considered the survival time or time-to-event (Machin et al., 2006). Survival analysis relies on censorship for accurate and reliable statistical analyses. In livestock, using the age at puberty for example, a left censored study would censor animals that had reached puberty prior to the beginning of a study; whereas a right censored study would censor animals that had not reached puberty by the end of the study. Right censoring is the most common type of censoring which occurs when a subject has not experienced the event by a set time. In the livestock industry, an example of a right censoring may be a cow who leaves the herd or dies after data for the study has been collected. Censoring allows for increased accuracy and reliability. Survival analysis is a versatile tool that can be applied to a wide variety of data sets and can comprehensively measure longevity and production traits of animals within a herd in comparison to their herd mates and species with accuracy and reliability.

Over time, survival analysis has become more complex. The idea and early methods of survival analysis originated when Weekly Bills of Mortality in London were published by John Graunt (1662). These bills consisted of numbers of deaths and their causes in London. Graunt compiled the data that had been collected to draw conclusions about disease mortality rates. His observations eventually led to the creation of the first life table. A life table is a statistical tool that contains survivorship data that is used to determine life expectancy based on a population's mortality rates Table(Mantel 1966). Conclusions were drawn from records of the time between when patients were diagnosed with a specific disease and their death; this data was used to compare mortality rates among diseases and years (Guo 2010). These life tables became the foundation of survival analysis for almost three-hundred years and continue to be one of the oldest statistical tools used (Cox 1972).

Survival analysis began to evolve with the introduction of the Weibull distribution (Rinne 2008). Waloddi Weibull, an engineer, presented his paper describing a continuous probability distribution that would allow for the ability to analyze life data and failure times. In 1951, this method was officially named after Weibull. The Weibull distribution model has gone on to become one of the most popular models in statistics today (Rinne 2008). The parametric Weibull distribution allows hazard rates to be modeled. Parametric models have a specific number of parameters (Rinne 2008). The Weibull distribution is a reliable and versatile procedure that can model a variety of types of data including skewed data and small sample sizes. The Weibull distribution function is an important tool for statistics due to its wide applicability (Weibull 1951). It is reliant on shape, scale, and location parameters (Rinne 2008).

Survival analysis continued to evolve when Edward Kaplan and Paul Meier published a method to estimate survival curves, survival probabilities and hazard rates (Kaplan and Meier 1958). As students, Kaplan and Meier each independently needed a way to be able to estimate survival rates to utilize data that included incomplete survival observations (Stalpers and Kaplan 2018). Following submissions of their independent work, a journal editor (John Tukey) convinced them to combine their work and publish one paper on how to handle incomplete observations (Stalpers and Kaplan 2018). Up to this point, various life table methods existed; however, these methods did not allow for incomplete data to be utilized effectively. Kaplan and Meier developed a method to utilize life table methods to estimate the probability of survival nonparametrically from survival times of both censored and uncensored records (Kaplan and Meier 1958). Nonparametric models are not reliant on a specified number of parameters and do not draw any assumptions regarding the distribution (Kaplan and Meier 1958). Thus, the Kaplan-Meier method was created to avoid censoring subjects who have not yet reached the established end point at the time of data collection (Stalpers and Kaplan 2018). This method allows for evaluation of the survival of a population and to test differences of cumulative survival among contemporary groups, with a graphical representation of the defined endpoint as a function of time (Goel et al., 2010). However, the Kaplan-Meier method has three assumptions and three limitations. The first assumption is that subjects censored at any one time have an equal survivability estimate as uncensored. The second assumption is survival probabilities are the same for subjects that entered at any point. The third assumption is the event happens at the endpoint (Goel, et al., 2010). The first limitation is the Kaplan-Meier method does not provide an effect estimate (relative risk) or the confidence interval to allow for comparison of survival among different contemporary groups (Stel et al., 2011). The second limitation is no adjustment for covariates or risk factors is allowed and events are assumed to occur independently (D'Arrigo et al., 2021). The third limitation is that data categorization is required (Rich et al., 2010). The Cox regression analysis can address these limitations.

Another step in the evolution of survival analysis methods occurred when D. R. Cox published the proportional hazard model in 1972 (Cox 1972). The Kaplan-Meier method can be applied to only one explanatory variable. The Cox proportional hazard model has become another popular statistical model (Cox 1972; Hazra and Gogtay 2017). The Cox proportional hazards model has become popular because it is a semiparametric model that uses an unspecified baseline hazard function and analyzes the individual effect of one or more explanatory variables (covariates) simultaneously in relation to an end event (Katz and Hauck 1993; Guo 2010). A semiparametric model is a blend of parametric and nonparametric models. The Cox proportional hazards model is semiparametric as it does not assume the baseline hazard is a parametric form (Katz and Hauck 1993). The Cox proportional hazards model assumes a linear relationship between the hazard and covariates is linear, which may be unrealistic. A second assumption of the Cox proportional hazards model is that it assumes hazard ratios are constant over time (Cox 1972; Guo 2010).

A second major approach to a regression analysis of censored data is the accelerated failure time model. Censoring poses major challenges in semiparametric analysis using this model (Cox and Oakes 1984). The accelerated failure time model is used to regress the logarithm of survival on time and thus relate the logarithm of the endpoint linearly to the effects that were included in the model (Cox and Oakes 1984). D. R. Cox stated that the accelerated time failure model can be more appealing than the proportional hazards model because in the proportional hazards model, the response variable does not always pertain to failure time, and it is assumed that the risk of failure is constant over time (Cox and Oakes 1984; Reid 1994). When applicable, the accelerated failure time model may deliver a more concise summarization of the data than the proportional hazards model.

Another survival analysis method is the non-parametric log-rank test. The log-rank test allows the comparison of survival trends of two or more groups that contain censored observations. The log-rank test is widely used in clinical trials to compare effectiveness of medical interventions in relation to an end event because multiple explanatory variables can be included (Hazra and Gogtay, 2017). An assumption for this test are that censored subjects have the same survival probability as uncensored subjects and the proportional hazards assumption that no group has a more favorable survival probability than any other groups (Hazra and Gogtay, 2017). The method allows for calculation of the Chi-square test statistic of the event time among groups because a limitation of this test is lack of survival comparison between groups without additional calculations. The results from the individual groups can be combined to derive a Chi-square test that can be used to compare the survival curves for each group (Rich et al., 2010).

Past Uses of Survival Analysis for Longevity in Beef Cattle

Historically, survival analysis was primarily used within the medical field to evaluate diseases, but over time has been applied to other fields. In the livestock industry, survival analysis has been particularly important for evaluating longevity and length of productive life. Herd life and ability to rebreed quickly are both economically important traits (Kachman 1999). The longer the animal is in the herd and consistently producing offspring, the more likely she is to be profitable for her owner. Since cattle are slower maturing and have a longer generational interval than many livestock species, cattle producers are at a relative disadvantage when compared to species with smaller generation intervals. Feed and labor costs can be high to raise a replacement heifer, so longer cow longevity leads to a longer period over which the replacement cost can be amortized and the number of replacement females that are needed to maintain constant herd size is reduced. Szabó and Dákay (2009) reported average longevity of various breeds in Hungary from age at first calving to culling or censorship. The average age at first calving was 2.90 years of age. The average longevity reported was 10.3 years for Hereford, 8.1 years for Angus, 7.9 years for Simmental, 7.1 years for Charolais, 5.9 years for Limousin, and 5.2 years for Blonde d' Aquitaine. Rogers et al. (2004) reported that a composite beef breed containing ½ Red Angus, ¼ Charolais and ¼ Tarentaise had a mean longevity of 967 days (2.65 years) between first calving and last weaning with a standard deviation of 743 days (2.04 years). The cattle studied by Rogers et al. (2004) were in a management system that included a cull for age criterion which increased the censoring in that data set. In the cattle industry, survival analysis typically utilizes either a Weibull model or a Cox proportional hazards model. Survival analysis has been used in numerous studies and been applied to data that includes age at first conception, age at first calving, heifer pregnancy rates (Pereira et al., 2007) and longevity (Caetano et al., 2016; Morales et al., 2017) as well as heritability estimation and genetic correlations between conformation traits and longevity (Vollema and Groen 1997).

Environmental effects such as management practices and genetics can affect longevity (Clasen et al., 2017). Taking these environmental effects into consideration may help explain variation in cow longevity when analyzing data across different farms and regions. Overall, an animal's ability to reproduce can impact the risk of culling and longevity. Biological factors affecting longevity include both health related factors and non-health related factors (Hess et al., 2005, Clasen et al., 2017). Some of the most important factors are those related to the cow's ability to reproduce. As a result of management decisions, a cow that fails to reproduce may be culled from the herd functionally ending her life. However biologically, the most fertile cows may have shorter lifespans due to the trade-off between fertility and lifespan (Kirkwood 1977; Williams 1957). Nutritionally, animals prioritize their survival, followed by reproduction and finally production (Hess et al., 2005; Sejrsen 1994). An organism's body is most concerned with keeping it alive (Hess et al., 2005, Sejrsen 1994). An animal's genetic makeup also plays an important role in longevity; however, longevity relies more heavily on environmental influences than genetics (Clasen et al., 2017). Longevity is a complex trait that is affected by both functional and productive traits (Clasen et al., 2017). Ultimately, an animal's genetic performance is also affected by genetic-by-environment interactions (Berry et al., 2014). Production traits are often more heritable than reproductive traits, but both traits are important for the growth and success of the offspring (Clasen et al., 2017). Although conformation is not as important in beef cattle as dairy cattle, genetics affect conformation (Morek-Kopec and Zarnecki, 2012). For example, it is important that a cow has a functional udder to raise a growing and healthy calf. Reproductive traits are lowly heritable, but important determinants of performance and longevity of a cow. Health traits can be of equal value to production and reproduction traits because a sick cow is unlikely to perform well overall. Illness decreases longevity (Alvåsen et al., 2018).

Management practices can be even more influential on performance (Beever 2006). For example, the time when heifers are bred affects dystocia. Younger heifers experience a greater incidence of dystocia, leading to decreased longevity (Fleck et al., 1980). Fleck et al., (1980) observed the relationship between reproductive performance and growth rate through 30 months of age with data from Hereford heifers, determining that at first parturition, heifers with high gains as yearlings had higher breeding efficiency, larger pelvic areas, larger calves, less calving difficulty, and higher breeding efficiency for the following season.

Nutrition provided post-weaning and reproductive management affect cow longevity (Beever 2006). Access to natural resources such as food and water sources are directly related to proper nutrition and an ample supply of water. Nutrition has a direct impact on development, onset of puberty, and reproduction, and an indirect impact on longevity (Fleck et al., 1980). Poor nutrition leads to poor performance and a higher risk of culling or death. Nutrition impacts both the development of the actual mother and the development of her calf (Sejrsen, 1994). Puberty is the time when an animal reaches sexual maturity and is physically capable of conceiving, carrying, and giving birth to offspring (Sejrsen, 1994). Nutrition has an inverse relationship on the age when a heifer reaches puberty. For example, an animal with proper nutrition may reach puberty at 12 months of age, whereas a malnourished or poorly managed animal may hit puberty around 18 months of age or later (Sejrsen, 1994). Heifers that reach puberty, become pregnant, and calve earlier may lead to shorter generation intervals because cows may be culled at earlier time points (Pereira et al., 2007). The length of the generation interval in cattle can be a challenge from an economic standpoint. It takes at least two years for a Bos taurus heifer to have her first calf and a cow to have enough calves to reach her breakeven point and be able to pay for herself (Snelling et al., 1995). Longevity is an important trait because a cow needs to be able to produce enough calves to pay for her heifer development costs. In the United States, the average breakeven number is six calves by the age of seven years if no opportunities to calve were missed (Boyer and Griffith 2018). If one calving is missed, the breakeven calf number goes to nine by the age of ten years (Boyer and Griffith 2018). The number of years needed for a cow to breakeven ultimately depends on input costs, cattle prices, breed, and country. For example, the breakeven point may be different in South Africa relative to the United States. Once a cow has reached her breakeven point, she will have paid for the costs of her development as a heifer (Morales et al., 2017). Bos indicus cattle typically have their first calf at three years of age.

Age at First Calving

Szabó and Dákay (2009) utilized a Cox proportional hazard model because this model allows for analysis of both categorical and continuous variables. The categorical variables used were herd, breed, calving season, calving difficulty, and sex of calf. The continuous variables were age at first calving and weaning weight. This study followed a total of 1800 cows of Simmental, Angus, Hereford, Charolais, Limousin and Blonde d' Aquitaine breeds born between 1980 and 2005 in Hungary. Their objective was to investigate longevity in relation to these seven variables. Longevity was defined as length of productive life, defined as the number of years from first calving until culling or censoring. The researchers concluded that breed, calving season, and calving difficulty affected longevity. The Blonde d’ Aquitaine and Limousine had the least longevity when compared to the other breeds. Simmental, Angus and Charolais were in the middle for breed impact on longevity. Hereford had the greatest longevity. Cows that calved in the autumn and winter months had an increased risk of culling when compared to those that calved in the spring and summer. Calving difficulty negatively impacted longevity. Age at first calving was not a significant variable contrary to the observation of Rogers et al. (2004).

Composite breed beef cows, comprised of half Red Angus, a quarter Charolais and a quarter Tarentaise germplasm have also been evaluated using survival analysis (Rogers et al., 2004). Their goals were to estimate risk factors affecting longevity of these animals, evaluate predictors for longevity, and estimate heritability of longevity. The data consisted of 1,379 composite cows born between 1982 and 1999 that calved at 2 years of age and that were traced back to the original Red Angus, Charolais and Tarentaise parents and about 33% were right-censored (Rogers et al., 2004). The length of productive life for each animal began on the date of the animal's first calving and ended on the weaning date of the dam's last calf record. Relationships between the length of productive life and the measured predictors were estimated with the Cox proportional hazards regression for survival analysis (Rogers et al., 2004). Risk factors evaluated were age at first calving, calf birth weight, calving difficulty, 200-day pre-weaning gain, breeding value for cow weight, maternal breeding value for preweaning gain and birth year of the cow. In this study, it was found that beef cows under the age of 730 days at first calving have less risk of being culled than cows older than 730 days of age at first calving ($P = 0.08$). Cows that experienced calving difficulty had a 58% increased risk of culling. The calf birth weight of the calf did not affect culling risk, independent of calving difficulty. Cows missing a 200-day pre-weaning gain value had double the risk of being culled than those with a recorded value. The missing value is likely due to the cow not weaning a calf. As the breeding value for cow weight increased, the risk of culling decreased, and as the maternal breeding value for preweaning gain increased, the risk of being culled increased. The risk of being culled based on the birth year of the cow varied significantly across years (Rogers et al., 2004).

Survival analysis was used to genetically evaluate age at first calving of Nellore cattle (Pereira et al., 2007). The goal of this study was to compare three approaches for evaluation of longevity to estimate heritability of sexual precocity in Nellore cattle. The evaluation approaches used were a Weibull mixed model and a censored linear model for age at first conception, and a threshold model for heifer pregnancy rates. Restricted breeding seasons and early exposure do not allow females to have a continuous opportunity to become pregnant leading to the necessity for censorship (Pereira et al., 2007). Heifers were exposed to bulls at 14 months of age and grouped into contemporary groups. At calving the next year, heifers were either censored or not censored based on whether they conceived a calf, where failure to calve was the censoring criterion. The mean heritabilities were 0.76 (survival), 0.44 (censored) for age at first calving, and 0.58 for heifer pregnancy, for the Weibull model, the censored linear model, and the threshold model, respectively. The latter model using heifer pregnancy as the dependent variable included heifers that failed to produce a calf. Heifer pregnancy rate and age at first conception were heritable using all these models. Substitution of the continuous trait for the binary trait in a threshold model increased precision, and the censored linear model found similar results to the Weibull mixed model. The censored linear model allows for analysis of censored observations, and possibly multiple traits. The Weibull mixed model also allows for use of time-dependent effects (Pereira et al., 2007). Although Pereira et al. (2007) utilized a censored linear model for age at first conception for statistical analysis of longevity data, linear models, however, are inadequate due to violations of the assumption of normality. Longevity data tends to be skewed based on censorship using linear models (Lagakos, 1979).

Heritability of Longevity

Another example of using survival analysis as a tool in beef cattle breeding is the use of age at last calving as an indicator trait for longevity. For example, survival analysis was used to estimate heritability and breeding values for longevity in the Nellore breed based on the age at last calving (Caetano et al., 2016). For this study, survival analysis with the proportional hazards model and a Weibull distribution were used. All the cows considered were born after 1998. Censoring was based on the difference between the date of last calving of the cow and the date of the last calving on the farm, which predicted reproductive efficiency (Caetano et al., 2016). Cows were censored once the interval between age at last calving and last calving on the farm was greater than 36 months. Using the Weibull model, the estimated heritability of longevity was 0.25 with a reliability of 0.997. Age at last calving may be used as a selection criterion since cows with higher age at last calving breeding values had fewer calves. The bull's breeding value plays a role in his daughter's risk of failure to produce a calf (Caetano et al., 2016). Breeding values for age at last calving consisted of a distribution with a mean of −0.03 months, minimum of breeding value of −1.585 months and maximum of 1.04 months. The mean breeding value for the risk of failure (death or culling) was 0.98 indicating that there was a 2% less risk of failure than the base group (risk of 1.0). The 95 % confidence range of the breeding values for the risk of failure was −0.46 to 0.26. Females with lower breeding values for failure could cause future improvement in the herd (Caetano et al., 2016). Caetano et al. (2016) also found a negative genetic trend for age at last calving (−0.0067) in relation to risk of leaving the herd, indicating that every year the risk of failure decreased an average of 0.67% per year.

Heritability of longevity was estimated in Retinta cattle. Heritability was estimated for length of an animal's true life, length of productive life and number of calves produced (Morales et al., 2017). Initial editing criteria excluded cows with an insufficient reproductive history, whose age at calving was less than 20 months or greater than 42 months, and whose records fell outside of three standard deviations in either direction from the average calving interval (Morales et al., 2017). Multiple environmental factors affected longevity of Retinta cattle and producers can increase the length of productive life by paying attention to age at first calving. Herd, season and year of cow birth, calf breed, and season and year of calf birth also affected longevity. Heritability estimates were 0.142 ± 0.01 for both length of true life and length of productive life, and 0.302 ± 0.01 for number of parturitions. The estimated additive variance ± s.e. was 0.292 ± 0.01 for all three traits. The number of calves produced had the highest heritability and therefore was the most reliable trait to select for in relation to longevity (Morales et al., 2017).

The Rogers et al. (2004) study referenced above also found that heritability of functional longevity was estimated at 0.14 and true longevity was estimated at 0.11, which is relatively low. As a result of this study, calving difficulty appears to be the largest risk factor for culling, and longevity was lowly heritable (Rogers et al., 2004). Genetic improvement of longevity is challenging because of the length of generation intervals, low relative heritability (Rogers et al., 2004). Caraviello et al. (2005) estimated heritability for longevity to be 0.18 in Jersey cattle. Martínez et al. (2004) found heritability estimates between 0.05 and 0.15 in Hereford cattle for length of productive life, where estimates varied depending on how productive life was defined. González-Recio and Alenda (2007) estimated heritability of functional longevity of 0.11 ± 0.01 in Holsteins using a sequential threshold-linear censored model.

A prototype system for national cattle evaluation of sustained reproductive success was developed by MacNeil and Vukasinovic (2011) utilizing survival analysis. The goal of this study was to identify sires whose daughters would maintain calving intervals that were consistent with annual calving. Data analyzed included 36,866 Hereford females born between 2001 and 2007 and 38.4% were right-censored. Females that were transferred between herds and those that became embryo donors were treated as censored. The heritability of sustained reproductive success was estimated at about 0.05. Survival analysis was used using grouped data models. Grouped data models are a special case of proportional hazard models that groups failure times into intervals and were used because reproductive success was defined by index values (Mészáros et al., 2010). The researchers have no doubt more data accumulated will improve the effectiveness of this genetic evaluation and allow for development of improved genetic evaluation and prediction methods that will help breeders make informed economic decisions (MacNeil and Vukasinovic, 2011).

Longevity varies based on breed. Dákay et al, (2006) studied differences in age at first calving, age at culling and longevity in different breeds of beef cows in Hungary. They observed greater longevity (the difference between age at first calving and the age at culling) in Hereford (9.08 years), Hungarian Grey (8.59 years) and Angus (8.29 years) cows, lesser longevity in Charolais and Limousin cows (7.91 and 7.81 years respectively) and still shorter longevity in Limousin crossbred (Simmental x Limousin F1) cows (5.55 years). Hereford crossbred cows (Simmental x Hereford F1) had the longest productive life (10.79 years) (Dákay et al, 2006). The results of this study indicated that there are potential differences between individual breeds in relation to longevity. Rohrer et al. (1988b) collected data from five purebred and twenty-five crossbred groups of heifers. The study lasted from January 1973 until June 1987. Cows were removed throughout the experiment due to death, poor health, injury, and soundness issues (eyes, udder, and legs), reproductive failures, and experimental culling (for another study) (Rohrer et al., 1988b). Nonlinear regression using a Weibull distribution was conducted to produce survival curves for the different breed types. Differences were observed among breeds in functional longevity with breed effects of 497.5, 407.9, 384.3, -546.0 and -743.6 days for Angus, Brahman, Hereford, Holstein, and Jersey, respectively (Rohrer et al., 1988b).

Genetic Correlations Between Longevity and Conformation Traits

The relationship between longevity and conformation traits was evaluated in Dutch Black and White dairy cattle (Vollema and Groen 1997). The cattle were born in 1978, 1982, and 1989 plus 1990. Survival analysis was used to estimate heritability for longevity and the relationship between functional longevity and conformation traits. Longevity traits observed were number of lactations, herd life, and stayability until 36 and 48 months of age. Herd life was measured from birth until the last test day. Conformation traits considered were rear legs set, front teat placement, udder depth, suspensory ligament, and udder, feet, legs, and type scores (Vollema and Groen 1997). These traits are highly important in the dairy industry (Vollema and Groen 1997). The heritability estimates for functional longevity were divided by birth years and observations. Heritability estimates for the number of lactations of cows born in 1978 was 0.08 and in 1982 was 0.06. Heritability estimates for herd life were 0.09 for the 1978 group and 0.07 for the 1982 group, and heritability estimates for stayability until 36 months of age were 0.02, 0.01, and 0.03, for the 1978, 1982 and 1989 plus 1990 groups respectively. The heritability estimates for stayability until 48 months of age for the 1989 plus 1990 group was 0.02. Conformation of the udder, feet and legs had stronger genetic correlations with longevity than the other conformation traits evaluated. The genetic correlation between udder score and stayability until 36 months was +0.78 and between udder score and stayability until 48 months was +0.93. The genetic correlation between feet and leg score and 36-month stayability was +0.20 and udder score and 48-month stayability was +0.43. (Vollema and Groen, 1997). This research proved that some quadratic relationships between conformation traits and longevity existed, but most relationships were linear.

Varona et al. (2012) used the Cox proportional hazard model to conduct a survival analysis to investigate genetic correlation of longevity with growth traits, carcass traits, teat morphology, leg morphology, milk production, and docility in the Pirenaica beef cattle breed. Longevity was defined as the number of calves per female (15 calves maximum). Growth traits included calf birth weight, 120-day weight, and 210-day weight. Carcass traits were cold carcass weight, conformation, fatness, and meat color. Teat morphology included teat thickness, teat length and udder depth. Leg morphology included forward and backward legs. The survival analysis measured survival time in discrete-time intervals and a sequential threshold model was used. Independent bivariate

Bayesian analyses were also used between cow survival and each recorded trait. The mean estimate (± standard error) for the heritability of survival was 0.05 (± 0.01). No trait was found to be a clear indicator of survival, but positive genetic correlations were estimated as follows: 0.07±0.04 for 120-day weight, 0.12± 0.05 for birth weight, 0.10± 0.05 for 210-day weight, 0.15± 0.05 for cold carcass weight, -0.18± 0.06 for conformation, 0.33± 0.06 for fatness, and 0.27±0.15 for meat color (Varona et al., 2012).

All the above research examples contained an element of estimating heritability of longevity or sustained reproductive success with different phenotypes and explanatory variables. All confirmed that longevity was lowly heritable. The examples all utilized survival analysis but in slightly different ways. The primary approach researchers use to analyze longevity and fertility data was survival analysis because this analysis allows the utilization of censored animals, maximizing data resources. The two most common models were the Cox proportional hazard model and the Weibull model.

Inbreeding Depression

Genetics affect longevity. Homozygosity is the exact opposite of heterozygosity and can be caused by inbreeding. Inbreeding can have a negative impact on performance traits. This impact is known as inbreeding depression. Inbreeding depression is explained by two main hypotheses, the overdominance hypothesis and the dominance hypothesis. The overdominance hypothesis is when a heterozygous animal has superior fitness when compared to homozygous animals. The dominance hypothesis is when recessive alleles decrease fitness in relation to the dominant alleles expressed in heterozygotes (Davenport 1908; Bruce 1910; Jones 1917). Both hypotheses compare the fitness of homozygotes to heterozygotes. A study done in by Nuno Carolino and Luis Gama in Portugal observed the effects of inbreeding effects on Alentejana beef cattle. They found that increased inbreeding levels decreased number of calves a cow gave birth to in her life, calf weight, longevity and number of calves produced in a seven-year period. This study shows that inbreeding has a detrimental effect on longevity and fertility. Longevity and fertility are extremely important for the economic wellbeing of a cattle operation. MacNeil et al. (1989), also observed the effects of inbreeding and hybrid vigor by comparing linecross, topcross, inbred and control Hereford females. In this study, inbreeding negatively impacted reproduction and maternal performance. As expected, crossing inbred lines resulted in significant heterosis, whereas performance levels of the linecrosses were comparable to the control group (MacNeil et al., 1989). Higher inbreeding levels do not always lead to large amounts of inbreeding depression (Sumreddee et al., 2019). Inbreeding levels measured by pedigree and genomic information did not have a large negative effect on growth performance, even for inbreeding levels of 16-30%, contrary to what was expected (Sumreddee et al., 2019).

Increased heterozygosity has been associated with improved overall performance (Sewalem et al., 2006). Heterozygosity is increased through crossbreeding. The increased performance of crossbred offspring relative to the average of the parental breeds is termed heterosis or hybrid vigor. Crossbreeding purebred lines combines the average genetic effects of both breeds while also taking advantage of hybrid vigor. Hybrid vigor is the exact opposite of inbreeding depression (Charlesworth and Willis, 2009; Pekkala et al., 2014; Bowman and Falconer, 1960; MacNeil et al., 1989). Many studies have found that longevity can be improved through crossbreeding because of hybrid vigor. Spelbring et al. (1977) studied hybrid vigor for maternal productivity in purebred Angus and Milking Shorthorn cows and reciprocal crossbreds, reporting that hybrid vigor improved percentage of cows retained by 18% over the first four lactations relative to purebreds ($P < 0.01$). Nunez-Dominguez et al. (1985) analyzed data from 328 straightbred Hereford, Angus and Shorthorn, and the reciprocal cross females born between 1960 and 1963 and determined that the crossbreds, on average, survived 1.4 years longer than purebreds (hybrid vigor = 16%). Rohrer et al. (1988a) studied data from 15 breed types produced in a five-breed diallel including Angus, Brahman, Hereford, Holstein and Jersey, reporting that the longevity of crossbred cows was greater than purebred cows ($P <0.001$). Cundiff et al. (1992) observed that during a 12-year lifespan crossbred cows would be expected to produce about one calf more than purebred animals.

Goals of this study

This study is based on data from the Afrikaner breed. Concern for the detrimental effects of inbreeding in the Afrikaner breed led to the use of Bonsmara as an outcross followed by repeated generations of backcrossing to Afrikaner. This endeavor came to be known as the infusion project. The first objective of this research was to establish the generational effects on longevity in the infusion project. Genetic studies of longevity in the Afrikaner breed are limited and integration of longevity as selection criteria into Afrikaner breeding programs is scarce. Thus, the second primary objective of this research was to conduct a genetic evaluation for longevity of Afrikaner cattle. Coincident with the accomplishment of this objective was an opportunity to evaluate the effects of age at first calving and season of birth on the longevity of Afrikaner females.

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Table 1.1. An example of a life table from Mantel (1966).

	Died	Survived	Total
Group 1	r_{1i}	N_{1i}- r_{1i}	N_{1i}
Group 2	r_{2i}	N_{2i}- r_{2i}	N_{2i}
Total	M_{1i}	M_{2i}	T_i

r: respective number of deaths
i: *i*'th time interval
N: number of individuals followed
M: total number of individuals in the respective column
T: overall total of individuals

CHAPTER 2: THE EFFECT OF THE AFRIKANER INFUSION PROJECT ON LONGEVITY: A SURVIVAL ANALYSIS[1]

ABSTRACT

The Afrikaner breed of cattle is indigenous to South Africa and due their hardiness has been used in forming several new composite breeds. In the 1980's, Afrikaner breeders became concerned about a perceived loss in fertility and their lack of attention to performance traits. The "infusion project" was developed to target shortcomings of the Afrikaner breed with the introgression of Bonsmara alleles into Afrikaner cattle. However, documented evidence of resulting changes in the fitness of Afrikaner cattle is scant. A survival analysis of the infusion project's impact on longevity has been completed with the Cox model. The first backcross generation (BC1) and the initial Afrikaner-Bonsmara cross generation (F1) had the lower risk ratios at 0.815 and 0.837, respectively, when compared to the purebred Afrikaner indicating their greater longevity. The second (BC2) backcross generation did not differ in longevity relative to the purebreds ($P \geq 0.05$). The infusion of Bonsmara impacted longevity in the short-term, possibly due to increased retained heterosis or the breed substitution effect. However, the effect on longevity diminished as the generations of backcrossing to Afrikaner progressed.

Keywords: backcross, Cox regression, selection decisions

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[1] Published as: Bot Steffl, A. M., M.G. Gonda, M.M. Scholtz, M.D. MacNeil. 2023. The effect of the Afrikaner infusion project on longevity: A survival analysis. Livestock Science 276, 105323. https://doi.org/10.1016/j.livsci.2023.105323.

INTRODUCTION

Afrikaner is a Sanga type (Bos taurus africanus) breed of cattle indigenous to South Africa and until the 1970's was the most abundant breed in the country (Pienaar et al., 2018). Afrikaner cattle are small to medium in size (mature cow weight 476 kg) with moderate maintenance requirements and are adapted to the environment of South Africa. Some adaptations include parasite and heat resistance, docility, and the ability to reproduce in harsh conditions (Scholtz et al., 2016). Because of its presumptive hardiness, calving-ease, fertility, moderate maintenance requirements, and carcass quality the Afrikaner has been a popular choice to serve as a base for developing composite breeds. Among the composite breeds that were developed from an Afrikaner base were Afrigus (Angus), Afrisim (Simmental), Bonsmara (Hereford and Shorthorn; also known as the Belmont Red breed in Australia), Hugenoot (Charolais), and Sanganer (Nguni) (Scholtz et al., 2016). In the 1970's, the number of Afrikaner cattle began to decline due to breeder observations of decreased fertility and reproduction from selection for show traits, and lack of attention to performance and production traits (Steenkamp & Tissier, 2016). To address the perceived problems within the Afrikaner breed, a so-called "infusion project" was initiated to introgress genes from Bonsmara into Afrikaner. The infusion project targeted fertility, low growth potential, and decreasing genetic variation while intending to maintain the favorable characteristics of the Afrikaner breed. Ideally Afrikaner females would be mated to Bonsmara bulls to produce an F1 generation and the resulting females would be bred to Afrikaner bulls to produce a first backcross generation (BC1). The BC1 females were again bred to Afrikaner bulls to produce a second backcross generation (BC2) (Vermaak et al., 2016). Initial observations were that

Bonsmara infusion improved fertility and weaning weights. Age at first calving was 37 days less in the F1 generation compared to the purebred animals with age at first calving also decreasing by six and four days in the BC1 and BC2, respectively, when compared to the purebred animals (Vermaak et al., 2016). Weaning weights also improved. The F1, BC1 and BC2 animals were from 7 to 13 kg heavier at weaning compared to the purebred animals (Vermaak et al., 2016).

This research was motivated by the previous observation of benefits resulting from the infusion of Bonsmara germplasm into Afrikaner. The objective was to compare longevity of cows that represented the infused generations with longevity of the purebred Afrikaner cows. Longevity is important because the longer cows remain in the herd the fewer replacement females are needed in order to sustain herd size (Nunez-Dominquez et al., 1985). In the present study longevity or length of life was defined as the time between when a cow was born and when she had her last calf.

MATERIALS AND METHODS

Data that pertained to the Afrikaner breed were recorded in the Integrated Registration and Genetic Information System (INTERGIS) (https://www.gov.za/agriculture-national-animal-recording-and-improvement-scheme) for 269,457 calves from 74,402 dams. The dataset for the infusion project was harvested from this database by identifying those dams whose progeny were coded as F1, BC1, and BC2. Records of the F1 females were subsequently inspected to verify that their dams were purebred Afrikaner and they were sired by a Bonsmara bull. The BC1 generation females were required to be progeny of F1 dams that were sired by a purebred Afrikaner sire. Finally, the BC2 generation descended from BC1 females that had been joined with purebred Afrikaner bulls. Contemporary groups were defined by the herd and year of birth of each cow. Purebred Afrikaner females from the same contemporary groups as the F1, BC1, and BC2 cows were chosen at random to comprise a control group. The final data set was composed of 2,544 cows born in 1995 or later: 1902 control cows, 269 F1 cows, 254 BC1 cows and 119 BC2 cows. Data for each cow also included herd, year of birth, and her length of life (days) measured as the difference between the cow's birthdate and the date when her last calf was born. Because the assumption that females failing to reproduce annually are culled by Afrikaner breeders is frequently invalid censoring was deemed to have occurred when a cow had calved after August 18, 2018, This cutoff date was two years prior to when the last observation contained in the original dataset was recorded.

The data were assessed for the appropriateness of the assumption of proportional hazards across generations using Schoenfeld (1982) residuals and were subsequently analyzed using the Survival Kit V.6.1 interface for R (Mészáros *et al.,* 2013). Hazards (β_i) $\pm$ SE, chi-squared (χ^2) values, and associated *P*-values (significance level $P = 0.05$) were all calculated using the interface. The χ^2 statistic (=square of estimate/standard error) for a Wald test of each regression coefficient β_i to test if $\beta_i = 0$. The risk ratios are the exponential of the estimate of the regression coefficient (Mészáros et al., 2013). Risk ratios for the fixed covariates were estimated using the Cox model. The Cox model is based on the proportional hazard concept that defines the hazard function of individuals as the probability an animal dies or is culled given that it is still alive just before time (t) (Mészáros *et al*., 2013). The fixed covariates were generation (i.e., control, F1, BC1 and

BC2) and herd-year. The dependent variable was length of productive life in days. The Cox model used to analyze survival data is the hazard function of an individual at time *t* expressed as:

$$\lambda(t)_{ij} = \lambda o(t) \text{ exp } [G_i + HY_j]$$

where $\lambda(t)$ is the risk of death (or culling) or hazard function for the dam with breed composition i and herd-year contemporary group *j* at time *t*, $\lambda o(t)$ is the baseline hazard function, G_i is the fixed effect of the i^{th} generation (control, F1, BC1 and BC2) and HY_j is the fixed effect of the j^{th} herd-year. The program automatically imposes constraints for each of the fixed effects such that the level of the effect with the largest number of uncensored failures has an estimate of zero. In this analysis, the control generation was set to zero, as was the selected herd-year class. The constraints allow for ease of interpretation and to calculate specific contrasts (Mészáros *et al*., 2013). A Kaplan-Meier survival function curve based on survival proportion was also created. The survival proportion was calculated for each generation as 1 minus the hazard function $\lambda(t)$ of an individual at time *t*:

$$\text{Survival proportion} = 1 - \lambda(t)_{ij}$$

Percent retained hybrid vigor (%RHV) was calculated for each generation as 1 minus the product of the breed *i* fractions from the sire (P_{si}) and dam (P_{di}):

$$\text{RHV} = 1 - (\textstyle\sum_i^n \ P_{si} \text{ x } P_{di})$$

where *n* is the number of breeds and breed types (4) (Falcolner & Mackay, 1996). Thus, the percentages of RHV were 57%, for the F1 females with each successive generation of backcrossing to Afrikaner reducing the estimated percentage of RHV by half (BC1 = 28.5%; BC2 = 14.25%).

RESULTS AND DISCUSSION

Breeders of Afrikaner cattle observed reduced fertility resulting in lowered reproductive rate and lack of attention to performance and production traits beginning in the 1970's (Steenkamp & Tissier, 2016). To address these perceived problems a decision was taken to broaden the Afrikaner gene pool by allowing breeders to use Bonsmara germplasm as a mild outcross. The Bonsmara breed was developed by Professor Jan Bonsma with the goal of developing a breed composition of 5/8th Afrikaner and 3/8th Shorthorn and Hereford (Scholtz et al., 2016; Makina et al., 2016). Bonsmara bulls considered ideal for outcrossing on Afrikaner were characterized by being well-muscled, with clear male secondary sex characteristics and a strong hump, short and shiny hair, thick skin, medium frame size, and strong maternal and direct breeding values for growth (Vermaak et al., 2016).

In the present data, about 10.5% (268) of the dams were right censored, meaning that they had not been culled or otherwise disposed of at the time the dataset was created. The percent of right censored animals was lower than many previous studies (e.g., Rogers et al., 2004; MacNeil & Vukasinovic. 2011). Although percentage of censored animals varied by the breed composition in the present study, with the more advanced generations of backcrossing having greater rates of censoring, the level of censored animals in this study is also lower than similar studies due to inclusion of more years of data (1995 to 2018). For the censored records, the last recorded birth of a calf occurred when the cow was from 548 to 5456 days old. A total of 2283 dams were uncensored. Their minimum failure time was 637 days (1.75 years), the maximum was 6327 days (17.3 years), with the median longevity being 2200 days (6.0 years). Estimates shown in Table 2.1 from the analysis that simultaneously fit herd-year effects indicate the Bonsmara x Afrikaner F1 and BC1 crosses were at significantly lower risk of being culled relative to purebred Afrikaner (Table 2.1). The F1 females were at 1.19 (1/0.837) less risk of being removed from a herd while the BC1 females had a 1.23 (1/0.815) lower risk of culling or death. Longevity of the BC2 generation was not significantly different from purebred Afrikaner cows. However, this latter result should not be considered as being definitive due to the low numbers of animals in the BC2.

The Kaplan-Meier plot indicates that most dams remained in the herd until at least three years of age (1,095 days; Figure 2.1). However, this result is expected as cows were identified as being in the cohort of animals under study by producing a calf and Afrikaner cows primarily produce their first calf at around 3 years of age (Bergh et al., 2010). By six years of age, the probability of remaining in the herd drops to approximately 50%. Only about 25% of dams are expected to remain productive until nine years of age. Longevity at 25% survival was 3,837 days for the controls, 4,211 days for the F1, 4,457 days for the BC1 and 4,299 days for BC2 (Figure 2.2). The Kaplan-Meier curves differed by generation of the infusion project (Log-rank $\chi2 = 23.8$, $P < 0.001$). The confidence intervals around these curves overlap each other throughout much of the range of the data, which may explain why the F1 had lower longevity at higher % survival. At 4000 days of life (~11 years), the survival proportions for the control, F1, BC1 and BC2 females were 0.221, 0.257, 0.398 and 0.294.

These results are consistent with expected percentage of retained hybrid vigor (%RHV) which is completely confounded with the Bonsmara direct additive genetic effect in these data. The F1 Bonsmara x Afrikaner had the highest predicted %RHV (57%) with each successive Afrikaner backcross reducing predicted %RHV by half (BC1 = 28.5%; BC2 = 14.25%). Heterosis can result in improvements in longevity (Spelbring et al., 1977; Nunez-Dominguez et al., 1985; Rohrer et al., 1988a; Cundiff et al., 1992) but these improvements are expected to diminish as %RHV decreases. Greater longevity in the F1 and BC1 crosses, but not in the BC2 backcross generations, is consistent with expected heterosis effects. However, heterosis effects were not directly estimated in this study. Differences in longevity might also be explained by differences in breed composition independent of heterosis effects. As developed, the Bonsmara was to include 62.5% Afrikaner genetics and 37.5% Hereford and Shorthorn (Scholtz et al., 2016). Recent genomic evidence estimates the breed composition to be 40% Afrikaner, 33% Shorthorn, 19% African zebu, and 5% Hereford (Makina et al. 2016). Therefore, the F1 generation is expected to be approximately 70% Afrikaner, with percentage of Afrikaner increasing by one-half with each succeeding backcross (BC1 = 85%; BC2 = 92.5%). Disentangling the heterosis effects from breed direct effects would require data from Bonsmara and from some additional crosses including the reciprocal Bonsmara-sired F1 and backcrosses to Bonsmara.

Crossbreeding has improved longevity in cows through hybrid vigor effects and through breed complementarity whereby relatively poor additive genetic merit in one breed is offset by the superior merit of a second breed (Dickinson & Touchberry, 1961; Spelbring et al., 1977; Nunez-Dominguez et al., 1985; Rohrer et al., 1988a; Cundiff et al., 1992). Dickenson and Touchberry (1961) observed the differences in longevity of purebred Holstein and reciprocal crosses of Holstein and Guernsey dairy cattle. The crossbreds had a significantly higher survival rate than the purebreds; 31% of Holstein cows were removed during the first lactation compared to only 15% of the Holstein-Guernsey crosses. Spelbring et al., (1977) studied purebred Angus and Milking Shorthorn cows and reciprocal crossbreds, reporting that heterosis improved percentage of cows retained by 18% over the first four lactations relative to purebreds ($P < 0.01$). Rohrer et al. (1988a) studied data from 15 breed types produced in a five-breed diallel including Angus, Brahman, Hereford, Holstein and Jersey, reporting that the longevity of crossbred cows was greater than purebred cows ($P <0.001$). Nunez-Dominquez et al. (1985) studied the effects of hybrid vigor on longevity in Hereford, Angus and Shorthorn, and the reciprocal crosses thereof and determined that the crossbreds, on average, survived 1.4 years longer than purebreds (hybrid vigor = 16%). Thus, during a 12-year lifespan crossbred cows would be expected to produce about one calf more than purebred animals (Cundiff et al. 1992). Although these studies showed a positive hybrid vigor effect on longevity, it is unknown if introgression of Bonsmara alleles into Afrikaner cattle would similarly improve longevity through effects of heterosis or the breed substitution effect.

Additive variation among breeds may also contribute to differences in longevity. Dákay et al, (2006) observed greater longevity in Hereford (9.08 years), Hungarian Grey (8.95 years) and Angus (8.28 years) cows, shorter in Charolais and Limousin cows (7.91 and 7.81 years. respectively) and still shorter in Limousin cows (5.55 years). Rohrer et al (1988b) likewise observed differences among breeds in functional longevity with breed effects of 497.5, 407.9, 384.3, -546.0 and -743.6 days for Angus, Brahman, Hereford, Holstein, and Jersey, respectively. Caraviello et al. (2005) estimated heritability for longevity to be 0.18 in Jersey cattle. Martínez et al. (2004) found heritability estimates between 0.05 and 0.15 in Hereford cattle for length of productive life, where estimates varied depending on how productive life was defined. González-Recio and Alenda (2007) estimated heritability of functional longevity of 0.11 ± 0.01 in Holsteins using a sequential threshold-linear censored model. Taken together, these studies strongly support an effect of additive genetics on longevity. In this study, the inclusion of Hereford in the Bonsmara composite may have improved longevity in the F1 and BC1 crosses (Dákay et al., 2006; Rohrer et al., 1988b).

Further, Afrikaner breeders may not always objectively make selection and culling decisions based on breeding values or performance data. Although Afrikaner breeders were not specifically sampled, Nkadimeng et al. (2022) conducted a survey of smallholder farmers in South Africa and reported that 87% do not utilize heifer selection by age or lineage and 60% reported replacement heifers as open from first service after breeding season. The survey also indicated that 53% of the farmers do not cull non-productive and 80% do not cull old cows. Breeders may be biased toward retaining dams crossed with Bonsmara, leading to artificially higher longevity for the F1 and BC1 crosses. Culling decisions are complex. They are based in part on subjective factors determined by each breeder and herd. Decisions are also influenced by economic returns, and natural, social, and psychological factors (Haine et al., 2017; Dekkers, 1991; Dohoo & Dijkhuizen, 1993). Psychological factors may include biases and emotions. Breeders participating in the project knew which calves included Bonsmara genetics. These breeders may have expected Afrikaner with introgressed Bonsmara genetics to be better adapted to their environment, leading to breeders retaining these animals in the absence of objective evidence of improved performance. Infused animals may have also possessed a different phenotype than purebred animals. Blinded experiments reduce this type of bias. However, a blinded experiment here would have been impractical. Breeders are usually actively involved in controlling mating decisions and most would balk at losing control of these decisions.

CONCLUSIONS

At the outset of the project, it was expected that the increase in genetic variation resulting from crossing with Bonsmara would result in lasting gains in the productivity and fitness of the Afrikaner population. Results from this analysis indicate the infusion project had the anticipated short-term impact on longevity. The increased longevity of infused cows being influenced by retained hybrid vigor or perhaps the breed substitution effect is in line with results of previous studies. The F1's and BC1's had the lowest risk ratios and greater longevity than the later backcrosses and controls. The BC2 generation trended back towards the purebred Afrikaners suggesting continued generations of backcrossing might not be effective for maintaining the short-term gains in longevity.

ACKNOWLEDGEMENTS

The author would like to thank the South Dakota Agricultural Experiment Station for supporting this work; and the Afrikaner Breeders' Society for allowing access to the data.

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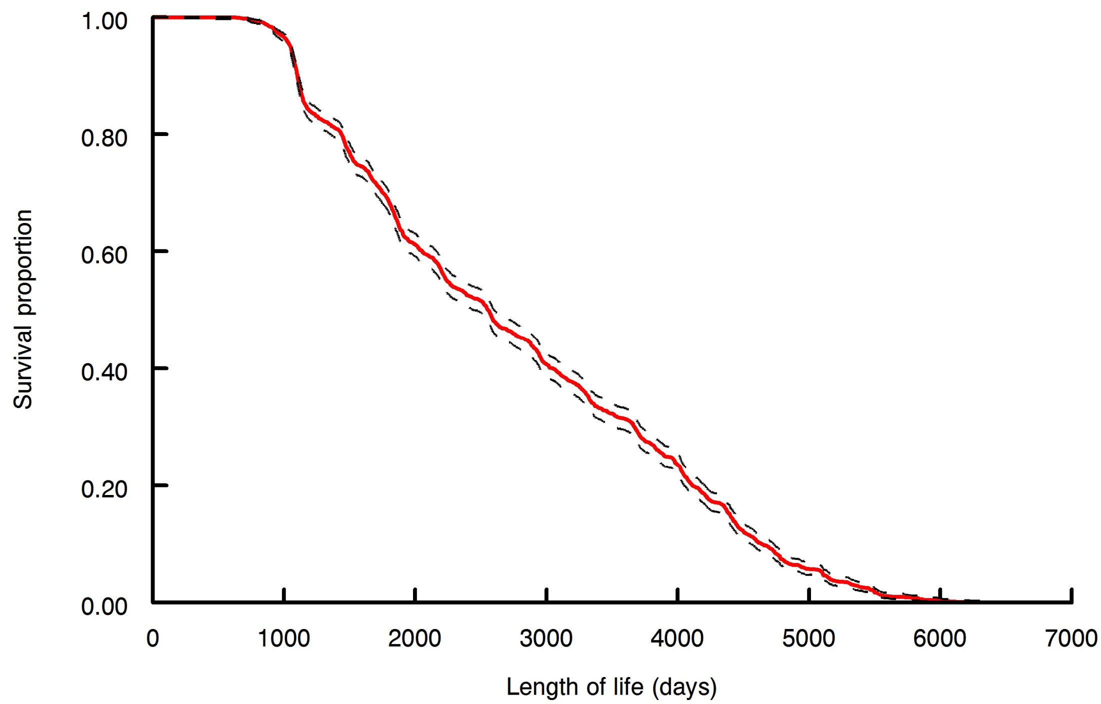

Figure 2.1. Kaplan-Meier survivor curve (solid red line) and 95% confidence interval (dashed black lines) for cows included in the Afrikaner infusion project based on the interval from the birthdate of the cow to the birthdate of her last recorded calf

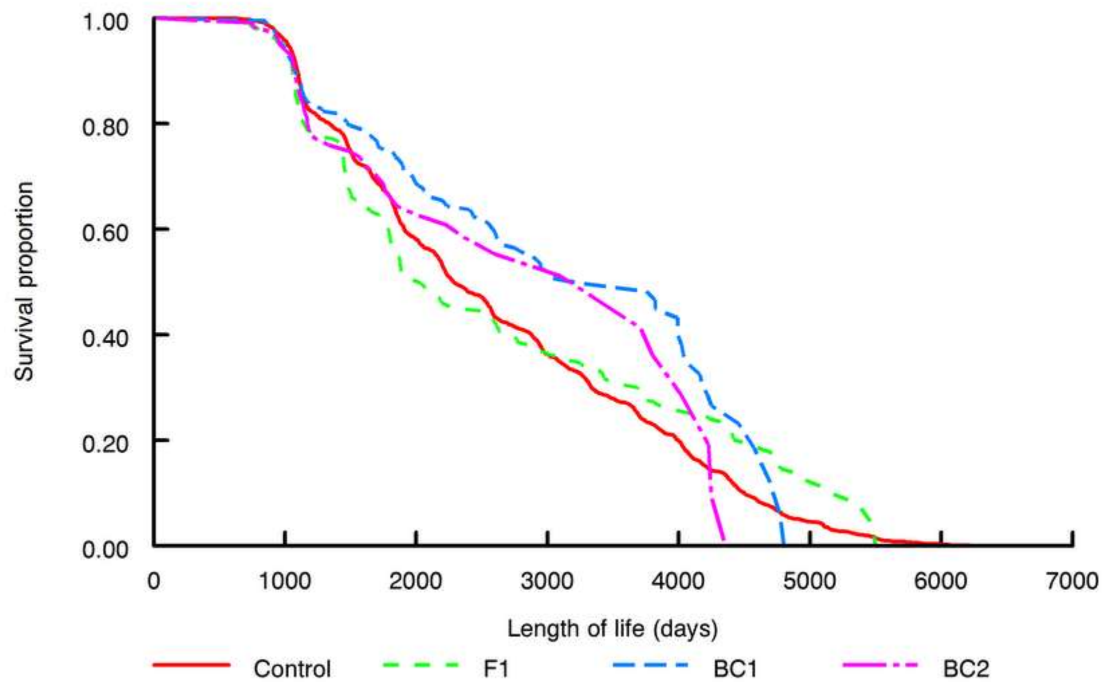

Figure 2.2. Kaplan-Meier survivor curves of for Bonsmara x Afrikaner (F1), Afrikaner x F1 (BC1), and Afrikaner x BC1 (BC2) cows in the different generations of the infusion project based on the interval from the birthdate of the cow to the birthdate of her last recorded calf.

Table 2.1. Estimates of average length of life and risk ratio for cows of different breed compositions.

Breed Composition[1]	Hazard	Standard error	χ^2	*P*-value	Risk ratio	Number animals	Number failures
Control	0.000				1.000	1902	1901
F1	-0.178	0.085	4.36	0.037*	0.837	269	219
BC1	-0.205	0.101	4.11	0.043*	0.815	254	116
BC2	-0.015	0.161	0.01	0.925	0.985	119	47

* $P \leq 0.05$

[1]= Control: Purebred Afrikaner; F1: Bonsmara sire x Afrikaner dam; BC1: Afikaner sire x F1 dam; BC2: Afrikaner sire x BC1 dam

CHAPTER 3: AFRIKANER LONGEVITY: A SURVIVAL ANALYSIS

ABSTRACT

The Afrikaner breed of cattle is indigenous to South Africa and due to their hardiness was once the most popular breed amongst farmers. Our objective was to estimate environmental effects (age at first calving, season) and genetic variance affecting longevity in Afrikaner cattle using survival analysis and a Weibull model. Age at first calving impacted longevity as younger age at first calving was associated with decreased longevity, possibly due to the incidence of calving difficulty in relation to heifer size. First calf heifers with an age between 640-730 days had a relative risk (RR) of 1.22 meaning a greater risk of leaving the herd than those that were 731 days or older. The group with the lowest risk was between 1361-1450 days of age (RR = 0.89). Season of birth impacted longevity as winter born calves (June-August) had increased longevity. The risk ratio for the lowest risk (winter months) was 1.3 and the highest (summer months) 1.65. Longevity in Afrikaner cattle was lowly heritable with an estimated heritability of 0.083. Although longevity was lowly heritable, sufficient genetic variation was uncovered to justify selection for this trait. The year of birth also impacted longevity.

Keywords: Afrikaner, longevity, calving season, age at first calving, heritability

INTRODUCTION

Afrikaner is a Sanga type (*Bos taurus africanus*) breed of cattle indigenous to South Africa (Pienaar et al., 2018). Afrikaner cattle are small to medium in size (mean mature cow weight 476 kg) with moderate maintenance requirements and are adapted to the environment of South Africa. Some adaptations include parasite and heat resistance, docility, and the ability to reproduce in harsh conditions (Scholtz et al., 2016). Because of its presumptive hardiness, calving-ease, fertility, moderate maintenance requirements, and carcass quality, the Afrikaner was once the most popular breed of cattle in South Africa and has been a popular choice to serve as a base for developing composite breeds (Pienaar et al., 2018, Scholtz et al., 2016). In the 1970's, the number of Afrikaner cattle began to decline due to breeder observations of decreased fertility and reproduction, presumably from selection for show traits and lack of attention to performance and production traits (Steenkamp and Tissier 2016).

Longevity in beef cattle is an economically important trait (Forabosco et al., 2006). It is directly related to the quantity of saleable products that are produced and production efficiency (Van Melis et al., 2007). Longer lived cows also necessitate retaining fewer replacement heifers (Núñez-Dominguez et al., 1985; López de Maturana et al., 2007; Brzáková et al., 2019), increase the potential number of calves produced by each cow (Morales et al., 2017) and increase the number of high producing mature cows (Rogers et al., 2004). Cows with longer productive lives are more profitable because of the reduction in the cost of raising replacement females as fewer replacements are needed to sustain herd size; the number of replacement females must offset those that are culled or open to maintain a constant number of cows in production (Szabó and Dákay 2009; Schmidt et al., 2017; Rogers et al., 2004; Nunez-Dominquez et al., 1985; Tanida et al., 1998).

The genetic evaluation of longevity is impacted by its late life expression, censoring, and non-normality of data. Linear models are ineffective for statistical analysis of longevity data and the data violate normality assumptions (Lagakos 1979). Additionally, survival analysis using a Weibull proportional hazards model has been found to be more accurate than linear models for analysis of longevity data (Caraviello, Weigel and Gianola 2004). Dams still in production could be classified as having a complete record or removed from the analysis but these approaches would bias estimates of longevity (Ducrocq 1994). To overcome these issues and reduce bias, survival analysis techniques can be used for the genetic evaluation of longevity (Ducrocq et al., 1988). Genetic studies of longevity in the Afrikaner breed are nonexistent and integration of longevity as selection criteria into Afrikaner breeding programs is scarce. The objective of this research was to complete a genetic evaluation for longevity of South African Afrikaner cattle based on recorded calving events. Using a Weibull proportional hazards model, genetic and environmental effects on longevity were estimated.

MATERIALS AND METHODS

Data that pertained to the Afrikaner breed were recorded in the Integrated Registration and Genetic Information System (INTERGIS) (https://www.gov.za/agriculture-national-animal-recording-and-improvement-scheme) for 75,625 dams of 275,144 calves. Data for each cow included dam birthdate, birthdate(s) of calves produced by each dam, and herd. Longevity was defined as the time interval (days) between the dam's date of birth and the date when she produced her last recorded calf. If 30 months had not elapsed between the dam's last calf record and end of data recording (March 24, 2022), then the dam's record was treated as right censored. The male-to-female sex ratio was originally 40% male and 60% female when all records from the raw dataset were included. The ratio between males and females was closer to 50%:50% after 1979, suggesting selective reporting of female calves prior to 1979. Thus, dams that were born prior to 1980 were not included in the data that was analyzed. Females without a recorded calf and with an age at first calving less than 640 and greater than 1650 days were also removed to prevent inclusion of inaccurate records. The minimum number of animals per herd-year-season (contemporary group) was 3. The average number of animals per herd is 84 with a minimum of 3 and a maximum of 1784 over a 40-year span. The final data set was composed of an observed measure of length of productive life for 35,120 cows from 417 herds born in 1980 or later. For AFC, dams were placed into categories based on consecutive 90-day time intervals, starting with 640 days of age until 1,450 days. The final category included 200 days (1,451 to 1,650 days of age). The season in which a cow was born was also not explicitly part of the original data set but month of birth was split into four seasons: season 1 (December-February), season 2 (March-May), season 3 (June-August), and season 4 (September-November). Censoring occurred when the animal remained alive and still producing at the end of the observation period. The date used for censorship was March 24, 2020, two years prior to the last recorded date of birth in the original dataset.

A Kaplan-Meier survival function curve based on survival proportion was created with survival proportion (probability of survival) on the y-axis and the length of life in days on the x-axis. The survival probability P_t was as follows for each time point *t*, where time intervals were divided into very small periods.

$$P_t = \frac{N\ alive\ at\ beginning - N\ reached\ end\ of\ life}{N\ alive\ at\ beginning}$$

Data were further analyzed using the Survival Kit V.6.1 interface for R (Mészáros et al., 2013). Morales et al., 2017 successfully used this software to genetically characterize longevity and productive life of the Retinta beef cows using a Weibull proportional hazards model. Risk ratios (ratio of hazards) are the exponential of the estimate of the regression coefficient calculated (Mészáros et al., 2013). The Weibull model is based on the proportional hazard concept that defines the hazard function of individuals as the probability an animal dies or is culled given that it is still alive just before time (*t*) (Mészáros et al., 2013). The fixed covariates were herd-year-season of birth and age at first calving groups. The dependent variable was length of productive life in days, measured as the difference between the birth date of the cow and the date of birth for her last calf. The Weibull model used to analyze survival data is the hazard function of an individual at time *t* expressed as:

$$\lambda(t)_{ijk} = \lambda o(t) \exp\left[G_i + HYS_j + A_k\right]$$

where $\lambda(t)$ is the risk of death or culling for a dam with fixed effect of age at first calving class (G) i , herd-year-season (*HYS*) j at time of birth , and random effect of estimated breeding value of animal (A) k , and $\lambda o(t)$ is the Weibull baseline hazard function. The program automatically imposes constraints for each of the fixed effects such that the level of the effect with the largest number of uncensored failures has an estimate of zero and hence risk ratio of one (Mészáros et al., 2013).

A pedigree file containing all animals in the data set, consisting of three generations, was constructed. The pedigree file contained 48307 cows, daughters of 3924 sires and 26838 dams. The heritability of longevity was estimated for the Afrikaner breed using the variance ratio and the proportion of uncensored records (32,156):

$$h^2 = \sigma_A^2/(\frac{1}{p} + \sigma_A^2)$$

where p is the proportion of uncensored records and σ_A^2 is the estimated variance ratio (Yazdi et al., 2002).

RESULTS AND DISCUSSION

In the present data, about 8.44% (2964) of the dams were right censored, meaning that they had not been culled or died at the time the dataset was created. The percentage of right censored animals was lower than many previous studies due to more tolerant censorship criteria, lack of exhaustive recording of reproduction records, and wide range of years (1980-2020). Vollema and Groen (1998) collected data from 1985 to 1996 which included 139,006 dams from 1,294 small herds (< 200) and 116,579 dams from 431 large herds. The small herd mean censorship percentage was 33.5% and large herd mean censorship percentage was 35%. Rogers et al. (2004) analyzed 1,379 composite cows born between 1982 and 1999, and 33% were right-censored; censorship criteria included pregnant cows that left the project and records of cows that remained in the herd in 2001. These criteria resulted in many censored females. The average length of productive life of censored animals was 967 days, and the uncensored average was not reported. Szabó and Dákay (2009) analysed data from 1800 cows from six different breeds. In Szabó and Dákay (2009) 40% of the animals remained in the herd at time of analysis so were treated as right censored. MacNeil and Vukasinovic (2011) analyzed 36,866 Hereford females born between 2001 and 2007 and 38.4% were right-censored. In MacNeil and Vukasinovic, (2011) females that were transferred between herds and those that became embryo donors were treated as censored in addition to those that were deemed to be still in production at the end of the study.

In the present study, longevity (failure time) of the 2964 censored dams ranged from 669 to 6453 days and the average was 2312 days (Figure 3.1). A total of 32156 dams were uncensored. Their minimum failure time was 648 days (1.75 years), the maximum was 7320 days (20 years), and the average was 2335 days (6.40 years). In this study, most dams (>80%) were predicted to remain in the herd until at least three and a half years of age (1,277 days; Figure 3.1). However, by six years (2,190 days; Figure 3.2) of age, the probability of remaining in the herd drops to almost 50%. Only about 25% of dams are expected to remain productive until nine years of age. Szabó and Dákay (2009) observed survival probability of six different beef breeds: Hereford, Angus, Simmental, Charolais, Limousine and Blonde d' Aquitaine. The 50% survival probability after first calving for each of these breeds respectively were as follows: 9 years, 8 years, 7 years, 6 years, 5 years, and 4 years. Hereford had significantly greater estimated longevity than the other breeds. Limousine and Blonde d' Aquitaine were similar to each other and had the least estimated longevity when compared to the other breeds. At 0.50 survival probability the Blonde d' Aquitaine were expected to live 4 years passed first calving or about 2,519 days total (Szabó and Dákay 2009). At 2519 days of age, the Afrikaner dams have a survival probability of approximately 40%. The difference is likely due to differing production practices, available resources, and environmental factors of the Afrikaner breed versus the breeds in the Szabó and Dákay (2009) study.

Afrikaner heifers that have an AFC of 2 years of age (730 days; Figure 3.2) have a greater risk of being culled than those that are 3 years of age (1,095 days; Figure 3.2).

These results for age at first calving do not correspond with the observation of Rogers et al. (2004) wherein there was a trend for beef cows less than 730 days old at their first parturition to have less risk of being culled than those that were older at their first calving (Figure 3.2). This may be due to the different culling practices in the United States versus South Africa. Schmidt et al. (2017) observed a negative correlation between age at first calving and stayability (length of productive life) in Nellore dams stating selection of heifers for early maturity should have small but favorable influence on longevity. Rogers et al. (2004) concluded that calving difficulty may be an important risk factor for the early failure of cows. The incidence of calving difficulty is highest in 2-year-old heifers but also may be high in 3-year-olds of certain breeds (Berg 1979). Afrikaner, due to a slower maturing rate, is likely a breed that may have higher incidence of calving difficulty at a younger age. Breeders may be calving older heifers due to the perceived consequences of calving younger heifers to reduce incidence of calving difficulty, thus improving longevity (Hickson et al., 2010; Titterington et al., 2015; Twomey and Cromie 2023). The results of the present study are consistent with this observation as younger heifers have a greater risk of being culled than the heifers that are older at AFC.

The Afrikaner breed is commonly chosen by breeders because of their hardiness and adaptations (Pienaar et al., 2018; Scholtz et al., 2016). This breed survives on top of mountains in extensive arid sweetveld with low rainfall and mild winters while producing calves with respectable weaning weights (du Plessis, Hoffman and Calitz 2006). South Africa is likely to have less feed resources than in developed countries, thus the opportunity for farmers to have complete control over nutritional management may be limited. Lamega et al. (2021) completed a study regarding smallholder farms and the ability to minimize feed gaps between seasons. Of the respondents, 80% claimed to encounter feed gaps during the winter, 30% in the spring and 20% in autumn (Lamega et al., 2021). Due to limited energy and protein, heifers tend to grow slower. Thus, heifers who calve at an early age on average will be lighter than heifers that calve at the same age in developed countries. The pelvic area tends to be smaller in lighter heifers, increasing dystocia (Sejrsen 1994).

However, Afrikaner breeders may not always make culling decisions based on breeding values or performance data. Culling decisions are complex. They are based in part on subjective factors determined by each breeder and herd. Decisions are also influenced by economic returns, and natural, social, and psychological biases and emotions (Haine et al., 2017; Dekkers 1991; Dohoo and Dijkhuizen 1993).

In this study, the cows that were born between December and February (1.60 risk ratio; Figure 3.3) had the largest risk of being culled, therefore reduced longevity, whereas those born between June and August (1.30 risk ratio; Figure 3.3) lived significantly longer. When fixed breeding season is utilized in South Africa, it is recommended that cows be first exposed to bulls starting about 1.5 months after the first effective rainfall in October (Bergh 2004). This is anticipated to result in females being in good body condition with their calves being born starting about two months before the start of the rainy season. In these data, the vast majority of cows were born in the months of September – November (season 4; N = 16,962) and December – February (season 1; N = 11,388). Results of this study differed from those of Singh et al. (2011) wherein the season of birth did not have an obvious influence on longevity; however, the observation regarding period of birth was similar. Singh et al. (2011) observed different 3 different time periods: 1983-87, 1988-93 and 1994-99. Longevity and productive life were significantly influenced by period of birth whereas season of birth had no significant effect. Różańska-Zawieja et al. (2014) also observed similar results to our study; through the evaluation of 80,605 animals born between 1990-2011 of breeds in Poland: Limousine, Charolais, Hereford, Beef Simmental, Salers, Black Angus, and Red Angus. The animals were split into seasons of birth: the summer season (March-August) and the winter season (September-February). Cattle born in the winter season remained in the herd 180 days longer than those born in summer. Similarly, Afrikaner calves born in the winter months in South Africa (June-August) had greater longevity. The difference in birth seasons could be attributed to feed availability at weaning. Winter-born calves are less likely to face a feed gap during early development post-weaning as feed gaps are predominantly in the winter due to lack of precipitation; however, cows that calved just prior or during that period may be impacted by that gap during lactation (Lamega et al., 2021).

Heritability of longevity as estimated from the South African Afrikaner data was 0.083. This estimate was similar to several estimates that were found in the literature: 0.08 (Larracharte et al., 2021), 0.11 (Mészáros et al., 2013b), 0.05 (MacNeil and Vukasinovic 2011), 0.14 (Rogers et al., 2004) and 0.037 (Brzáková et al., 2019). Improving longevity is expected to be a slow process due to low heritability. Longevity may be lowly heritable because it is a complex life-history trait that is impacted more by environmental variance (Price and Schluter 1991). Environmental factors could include but are not limited to age at first calving, season of birth, birth year, and resource availability. Although hard to predict, additive genetic variance of longevity may be sufficient to be able to improve longevity through selection and ensure breeding success (Price and Schluter 1991; Brzáková et al., 2019).

The risk ratio for the EBV or estimated breeding value of sires producing daughters in the 95th percentile was 1.091 with a projected length of life of 1920 days (Table 3.1. The 5th percentile has a lower risk ratio of 0.768 and are projected to live 2.58 years longer than the 95th percentile. This difference in longevity between sires in the top 5% and 95% EBV ranking suggests that, despite low heritability, substantial additive genetic variance for this trait is present in Afrikaner cattle. Lower accuracy and number of uncensored daughters for sires ranked near the top of the breed for longevity indicate less longevity performance data is available for these sires. Fewer uncensored records are available on sires with high longevity EBVs because their daughters are less likely to be culled, resulting in lower accuracy.

The environmental trend in longevity of Afrikaner cattle as indicated by the risk ratios shown in Figure 3.4 indicate large inter-annual fluctuations with a long-term general environmental trend toward decreased longevity. There was also a slight genetic trend in the risk ratio (b = -0.004) that was favorable but low, to a genetic increase in longevity (Figure 3.4). This is possibly due to increased breeder awareness of the need for selection of functional traits, including longevity (Vermaak et al., 2016). Larracharte et al. (2021) also estimated realized genetic gain for length of productive life in Angus cattle. In that study the genetic trend was also small but favorable for increased longevity. This study had similar results as the risk ratio decreased over time indicating a longer length of productive life. Selection for longevity takes time due to a lengthy generation interval, and longevity is lowly heritable. Low heritability and longer generation interval make selection for longevity more challenging. However, the presence of significant additive genetic variation for this trait means response to selection for longevity is possible, even if improvements are slow.

CONCLUSIONS

Results from this analysis indicate that heifers with an age of first calving before 2 years of age were at higher risk of being culled. To avoid this risk, a minimum breeding age of 15 months is recommended. Heifers born in the winter months were at reduced risk of culling as cows, therefore a defined breeding season that allows calves to be born during the winter months would be ideal. Heritability of longevity is low, largely because of high environmental variance. Data suggests that additive genetic variance is still significant; leading to the conclusion that selection could improve longevity, even if improvements may be slow.

ACKNOWLEDGEMENTS

The author would like to thank the South Dakota Agricultural Experiment Station for supporting this work; and the Afrikaner Breeders' Society for allowing access to the data.

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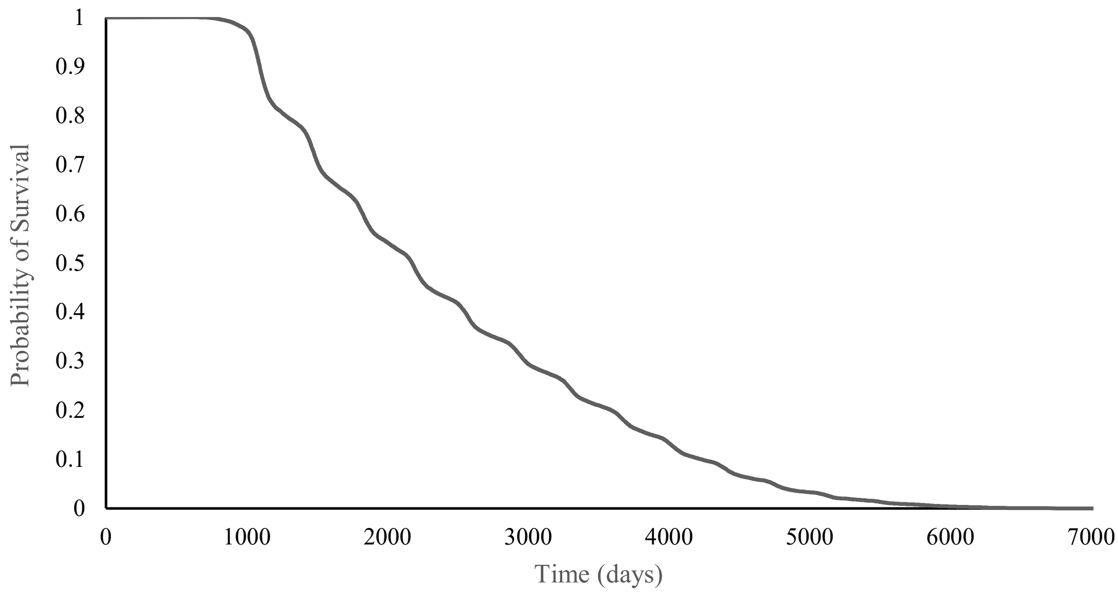

Figure 3.1. Kaplan-Meier survivor curve of dams from the dam's birthdate to end of productive life.

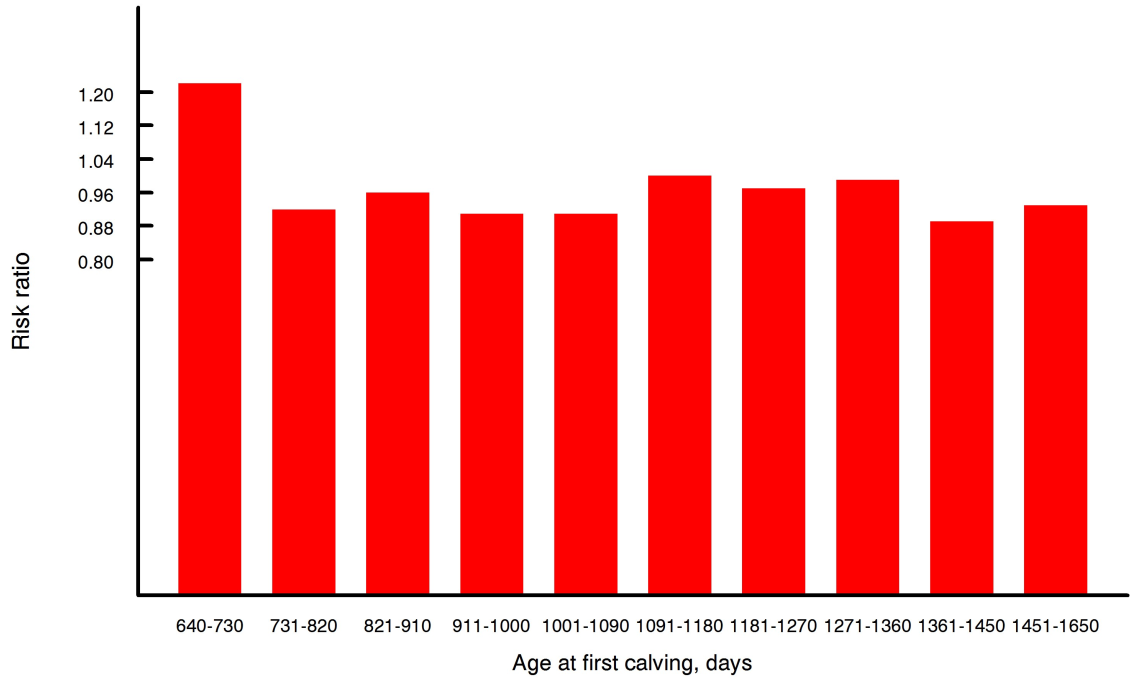

Figure 3.2. Effects of age at first calving on the risk ratio indicative of longevity in Afrikaner beef cows; greater risk ratios indicate a greater likelihood of being culled and hence reduced longevity.

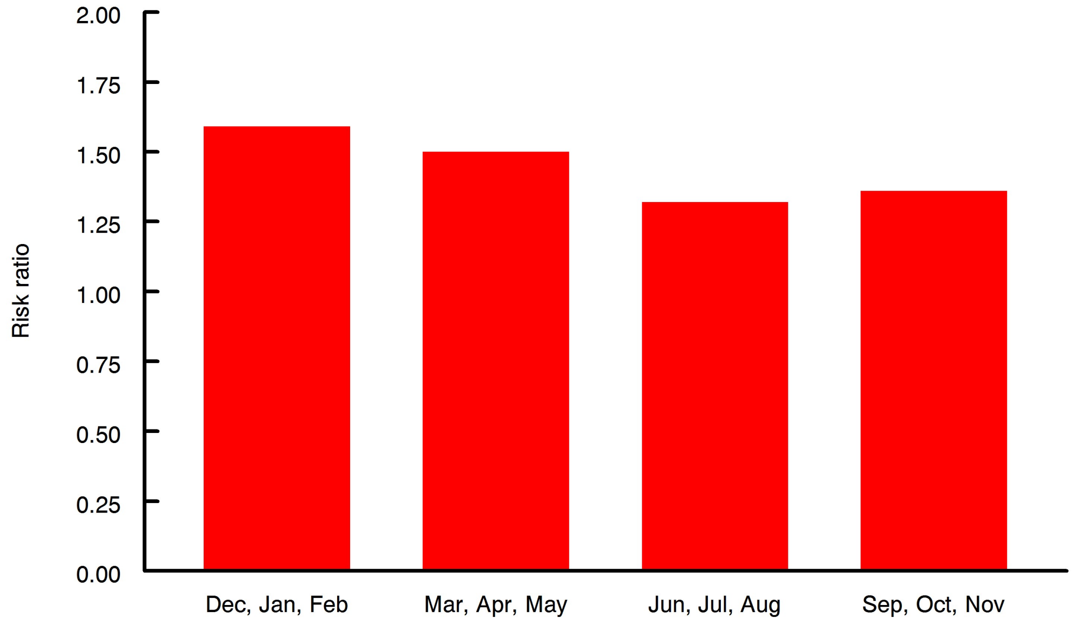

Figure 3.3. Effects of season of birth on the risk ratio indicative of longevity in Afrikaner beef cows; greater risk ratios indicate a greater likelihood of being culled and hence reduced longevity.

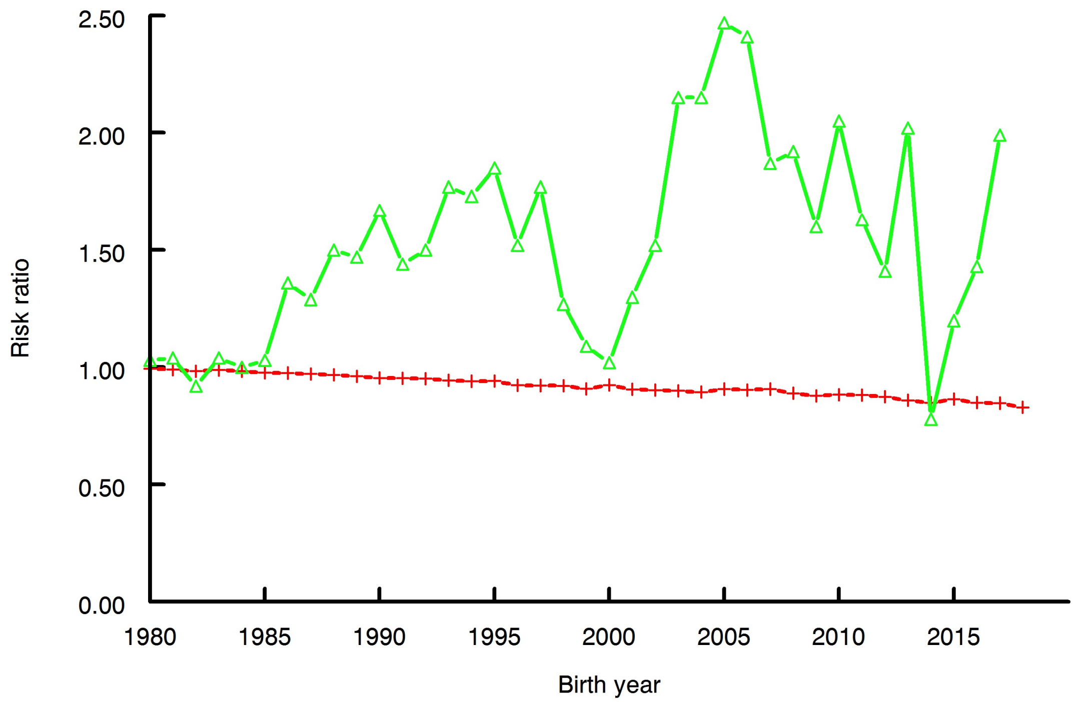

Figure 3.4. Environmental (green line) and genetic (red line) trends in the risk ratios indicative of longevity in Afrikaner beef cows; greater risk ratios indicate a greater likelihood of being culled and hence reduced longevity.

Table 3.1. Distribution of survival analysis results for Afrikaner sires producing daughters from 1980 to 2019.

Percentile	Risk ratio EBV	N uncensored daughters	Accuracy	Projected length of life
100	1.367	94	0.84	1116
99	1.156	54	0.76	1731
95	1.091	32	0.67	1920
90	1.056	24	0.62	2022
75	1.012	13	0.50	2150
50	0.961	6	0.37	2299
25	0.888	2	0.22	2511
5	0.768	1	0.16	2861
1	0.693	1	0.16	3079

CHAPTER 4: SUMMARYAND RECOMMENDATIONS

In the beef industry on a global scale longevity is an important economic trait. It is also a complex trait as it is influenced by numerous factors. In South Africa, the Afrikaner breed of cattle is an important indigenous beef breed and plays a role in development of composite breeds such as the Bonsmara. Following a perceived loss of production in the Afrikaner breed, South African animal breeders developed the Infusion project to introgress Bonsmara alleles back into the Afrikaner to increase heterozygosity and longevity. These results do not support the hypothesis that infusion of Bonsmara alleles improved longevity beyond the first backcross generation. The F1 generation and first backcross generation had improved longevity relative to the Afrikaner ($P < 0.05$), but longevity of the second backcross generation was not statistically different from the Afrikaner.

The third chapter of this thesis found that longevity was a lowly heritable trait in Afrikaner. The low heritability can largely be attributed to high environmental variance. Additive genetic variance was greater than zero indicating that selection could improve longevity, even if improvements may be slow. Afrikaner heifers with an age of first calving prior to 2 years of age were at greater risk of failure. To mitigate this risk, a minimum breeding age of 15 months is recommended. Heifers born in the winter months were at reduced risk of failure as cows, and therefore a defined breeding season for calving during the winter months would be ideal.

Future studies may compare longevity and the heritability of longevity in the Afrikaner breed to other popular beef breeds in South Africa; potential variables for comparison include herd, province, calving difficulty, sex of calf, birth weight, age at first calving, calving interval, and weaning weight. A specific example may be the comparison of longevity in the Afrikaner, Brahman, and Nguni breeds. This study could utilize age at first calving, calving interval, calving difficulty, and weaning weight. The results could help a producer choose which breed(s) may be the best option for their operation in terms of possible number of calves produced per cow as well as pounds of calf produced within her lifetime. Other options may include evaluation of longevity predictors like the Rogers et al. (2004) study, or an economic study regarding the cost of raising replacement heifers to determine the number of calves per cow required to justify replacement heifer costs similar to the Boyer and Griffith (2018) study. Rogers et al. 2004 evaluated risk factors of age at first calving, calf birth weight, calving difficulty, 200-day weaning weight, breeding value for cow weight, maternal breeding value for weaning weight and birth year of the cow to determine if any can be used to predict longevity. A similar study could be done with the Afrikaner breed to evaluate additional risk factors this project did not explore.