Received: 30 August 2023 | Revised: 17 December 2023 | Accepted: 29 December 2023

DOI: 10.1111/jbg.12847

ORIGINAL ARTICLE

Journal of Animal Breeding and Genetics WILEY

Longevity in South African Afrikaner cows as assessed through survival analysis

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Abstract

The Afrikaner breed of cattle is indigenous to South Africa and, due to their hardiness, was once the most popular breed amongst South African farmers, although in recent years their numbers have decreased. The goal of this study was to assess factors affecting length of productive life, defined as the interval between production of the first and last calf, in Afrikaner cattle using survival analysis. The data spanned 40 years with an observed measure of length of life for 29,379 cows from 374 herds. Relative to similar analyses, few ($n = 2964$; 8.4%) cows had records that were right censored. The median length of productive life of an Afrikaner cow was just less than 6 years. Cows that were younger at their first parturition had longer productive lives than those that were older at their first calving. Cows that were born in the period from December to February had shorter productive lives than those born between March and November. The estimated animal genetic variance of 0.266 resulted in a heritability estimate for length of productive life in Afrikaner cattle of 0.225. Thus, there appeared to be sufficient additive genetic variance in Afrikaner cattle to enable genetic improvement in their length of productive life.

KEYWORDS

age at first calving, genetic trend, heritability, length of life

1 | INTRODUCTION

Locally derived breeds show adaptation to their native environments (McIntosh et al., 2023). Afrikaner is a Sanga type (*Bos taurus africanus*) breed of cattle indigenous to South Africa (Pienaar et al., 2018). They 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 (Makina et al., 2015). Indigenous breeds are valued because of their presumptive hardiness, calving ease, fertility, moderate maintenance requirements and carcass quality. Thus, the Afrikaner was once the most popular

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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 1970s, the number of Afrikaner cattle began to decline due to breeder observations of decreased fertility, presumably from selection for show traits and lack of attention to performance and production traits (Steenkamp & Tissier, 2016).

Longevity in beef cattle is an economically important trait (Forabosco et al., 2006). It is directly related to the amount of saleable product that is produced and production efficiency (Van Melis et al., 2007). Longer lived cows also necessitate retaining fewer replacement heifers (Brzáková et al., 2019; López de Maturana et al., 2007; Núñez-Dominguez et al., 1985), 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). Garcia et al. (2015) found that annual net present value of beef cow production turned negative between 11 years for the Indu-Brazil crosses to 15 years of age in Nellore crosses, with Angus and Brahman crosses being intermediate. These outcomes were strongly affected by the number of times a cow failed to wean a calf and suggested breed affects cow longevity. Culling for failure to maintain an annual calving interval can markedly reduce observed longevity but confounds reproductive success with true longevity (MacNeil & Vukasinovic, 2011; Wellnitz et al., 2022).

Measures of longevity are not normally distributed but are skewed, typically having many early events and relatively few late ones (Clark et al., 2003). Longevity or survival time is thought to be most appropriately analysed using survival analysis (Ducrocq, 1997; Garcia et al., 2017; Olechnowicz et al., 2016). Survival analysis combines information from dead (uncensored) as well as live (censored) animals to allow for proper statistical treatment of censored records by accounting for nonlinear characteristics of the data (Vukasinovic, 1999). Studies of longevity for indigenous breeds are very limited, and integration of longevity as selection criteria into beef cattle breeding programs is scarce (Morales et al., 2017). The objective of this research was to conduct a genetic evaluation for the longevity of South African Afrikaner cattle based on recorded calving events. Coincident with the genetic evaluation was the opportunity to examine effects of age at first calving and season of birth, both of which are under a degree of managerial control, as well as providing some commentary on the quality of data that originates through self-reporting by breeders in a developing country.

2 | MATERIALS AND METHODS

Records of the existence of 275,144 Afrikaner calves from 75,625 dams recorded in the Integrated Registration and Genetic Information System (INTERGIS) (https://www.gov.za/agriculture-national-animal-recording-and-improvement-scheme) were obtained with the permission of the Afrikaner Breeders Society of South Africa for use in this research. The data that support the findings of this study are available from the corresponding author upon reasonable request; subject to the approval of the Afrikaner Breeders' Society. As these data were produced by the individual breeders who were members of the society, ethical clearance for this research was deemed unnecessary.

To potentially be included in this study, each heifer calf must have produced at least one offspring. The data for each cow also included her birth date, the birth date(s) of the calves she produced and the herd in which she was resident. Length of productive life was defined as the time between the date a cow gave birth to her first calf and the most recent record of her having given birth to a calf. Cows were assumed to have reached the end of their productive life when no calf was recorded for them during a period of 2.5 years following the birth of their most recent calf. Censoring occurred when the animal remained alive and producing at the end of the observation period. The date used for censorship was March 24, 2020, 2 years prior to the last recorded date of birth in the original dataset. Presumably, due to incomplete reporting, the sex of calves reported prior to 1981 was 92% female and 8% male. Because this incomplete reporting could bias the results of the genetic evaluation (Golden et al., 2009), all females born before 1980 were excluded from the data. After 1979, the sex ratio of the recorded calves was 50.9 to 49.1 males to females. The year was split into four seasons: season 1 (December–February), season 2 (March–May), season 3 (June–August), and season 4 (September–November). Females in herd–year–season contemporary groups of less than three animals were removed from the data as were those whose first calf was born outside the interval from 640 to 1650 days of age. In addition, females that did not have five paternal half-sibs in the data were also excluded. The data spanned a 40-year period with an observed measure of length of life for 29,379 cows from 374 herds born in 1980 or later. The average number of animals per herd was 78.6. Age at first calving was defined categorically as: 640–730, 731–820, 821–910, 911–1000, 1001–1090, 1091–1180, 1181–1270, 1271–1360, 1361–1450 and 1451–1650 days.

By dividing the time interval of interest into many small periods, a Kaplan and Meier (1958) survival function wherein the probability of survival (P) at time t is:

$$P_t = \frac{N \text{ alive at the begining} - N \text{ died in the interval}}{N \text{ alive at the beginning}}$$

The surv and survfit functions of R (R Core Team, 2021) were used for the computations.

Data were analysed using the Survival Kit V.6.1 (Mészáros, Sölkner, & Ducrocq, 2013) interface for R (R Core Team, 2021). Computational feasibility of the animal model for estimation of breeding values for cows using the Survival Kit V.6.1 was confirmed in the study of Mészáros, Kadlečík, et al. (2013). Risk ratios were estimated as the exponential of the estimate of the regression coefficient using the Weibull model (Mészáros, Sölkner, & Ducrocq, 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 at the immediately previous time (t) (Mészáros, Kadlečík, et al., 2013; Mészáros, Sölkner, & Ducrocq, 2013). The dependent variable was length of productive life in days, measured as the difference between the date when a cow gave birth to her first calf and the date of birth for her last calf. The model used was expressed as the hazard function of an individual at time t:

$$\lambda(t)_{ijk} = \lambda_0(t)\ \exp\left[C_i + \mathrm{HYS}_j + a_k\right]$$

where $\lambda(t)$ is the risk of death (or culling) for an animal associated with the ith fixed age at first calving class, the jth fixed herd–year–season in which the animal was born and the random estimated breeding value of the kth individual (a_k); $\lambda_0(t)$ 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 a risk ratio of 1. Estimates for the effects of year and season were the marginal unweighted means of the corresponding herd–year–season effects. The (co)variance among animal genetic effects was estimated based on a three-generation pedigree containing all animals in the edited data set. The pedigree contained 41,087 animals, descendants of 3078 sires and 24,083 distinct dams.

The heritability (h^2) of longevity was estimated for the Afrikaner breed using the estimated genetic variance (σ_a^2) and the proportion of uncensored records (p):

$$h^2 = \frac{\sigma_a^2}{\frac{1}{p} + \sigma_a^2}$$

(Mészáros, Kadlečík, et al., 2013; Mészáros, Sölkner, & Ducrocq, 2013; Yazdi et al., 2002).

3 | RESULTS AND DISCUSSION

In the Afrikaner data, 8.34% (2449) of the cows had right-censored records, meaning that they had not been culled or otherwise disposed of at the time the data set was created. The per cent of right-censored animals was lower than in many previous studies. For example, Rogers et al. (2004) analysed 1379 composite cows born between 1982 and 1999 and about 33% of them were right censored. This level of censoring can be explained, in part, by the transfer of cows to other research projects at 5 years of age. Szabó and Dákay (2009) analysed data from 1800 cows from six different breeds and found that 40% of the animals remained in the herd at the time of analysis and thus were treated as right censored. MacNeil and Vukasinovic (2011) analysed 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 analysing the longevity of 77,353 Nellore females born over a 15-year period, 21.0% of the cows were found to have right-censored records (Garcia et al., 2017). In an analysis of herd book data for Slovak Pinzgaurer cows spanning a period of 18.5 years, animals alive at the time of data collection, intentionally withdrawn from the milk recording and those from herds that decreased in size by more than 50% between consecutive years constituted 19.9% of the data and were considered right censored (Mészáros, Kadlečík, et al., 2013; Mészáros, Sölkner, & Ducrocq, 2013). This study included cows born between 1980 and 2019 (40 years), which is longer than the studies cited above. Thus, it may be concluded that the degree of censoring is to some degree inversely related to the length of time horizon over which the data were produced.

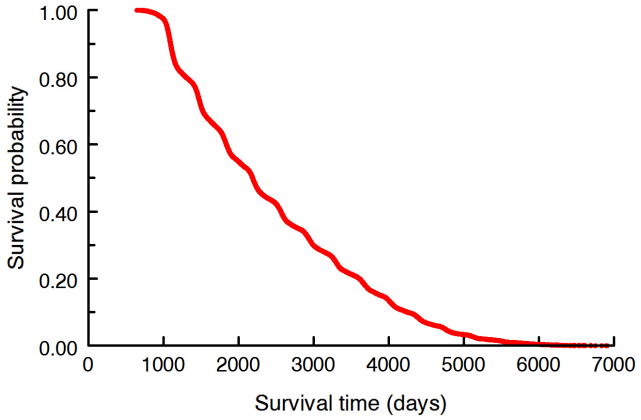

FIGURE 1 Kaplan–Meier survivor curve of Afrikaner cows from their date of first calving to the end of their productive life.

In this study, most of the cows (>80%) were predicted to remain in the herd until at least three and a half years of age (1277 days; Figure 1). However, by 6 years (2190 days) of age, the probability of remaining in the herd drops to just less than 50%. Only about 25% of dams were expected to remain productive until 9 years of age. Culling cows that fail to calve annually would be expected to shift the age distribution further towards younger females and

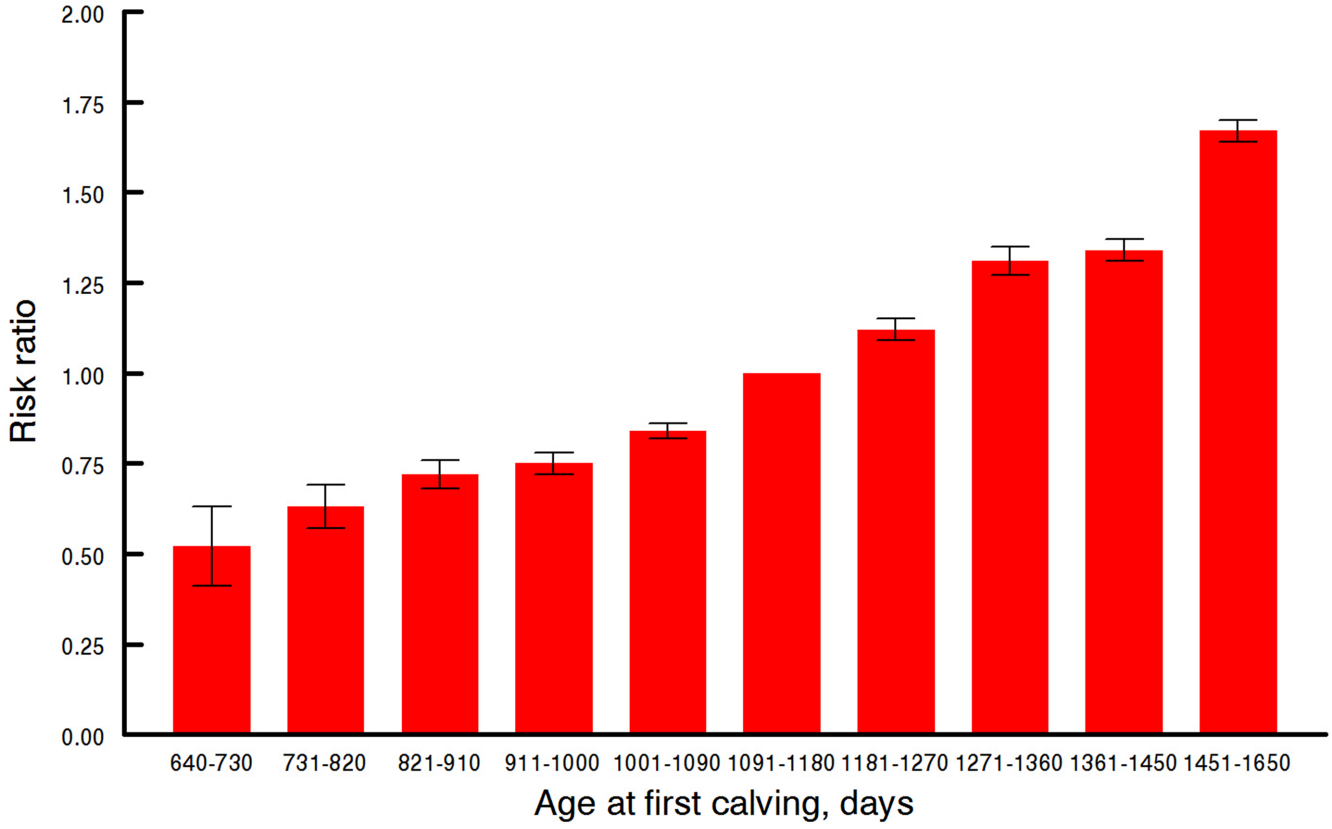

FIGURE 2 Effects of age at first calving on the risk ratio indicative of longevity in Afrikaner beef cows; greater risk ratios indicate a greater likelihood of being culled and hence reduced length of productive life.

may not be sustainable for Afrikaner cattle raised in harsh environments. In the present study, length of productive life of the 2449 censored dams ranged from the birth of their first calf to a maximum of 5385 days (14.75 years) and the median was 1072 days (2.94 years). A total of 26,930 dams were uncensored. Their minimum length of productive life was at the birth of their first calf, the maximum was 5887 days (16.13 years) and the median was 953 days (2.61 years). Relative to reports for longevity for other breeds, Szabó and Dákay (2009) observed that Blonde Aquitaine had a 50% probability of survival at less than 4 years of age, with Charolais and Limousin also having a 50% probability of survival at younger ages than the Afrikaner cows studied herein. However, in Szabó and Dákay (2009), Simmental, Angus and Hereford achieved a 50% probability of survival at older ages than the Afrikaner benchmark from this study. Dákay et al. (2006) observed Simmental × Hereford F_1 crossbred cows as being the longest lived (10.8 years), followed by Hereford (9.1 years), Hungarian Grey (9.0 years) and Angus (8.3 years) which had similar lifespans. They also observed that Charolais and Limousin had lifespans approaching 8 years, whereas Simmental × Limousin F_1 crossbred cows had the shortest lifespan (5.6 years). In general, the effects of heterosis on longevity have been shown to extend the length of productive life (Basarab et al., 2018; Núñez-Dominguez et al., 1985; Rohrer et al., 1988). Obviously, these comparisons among breeds are confounded by differences in environments, both between studies and within the studies conducted in Hungary. In addition, populations differ not only due to their inherent genetic make-up, but at as a result of differences in selection intensities, breeding objectives and selection histories among other factors. Thus, it is challenging to interpret breed differences without their being raised in a common environment under a uniform system of management, and even then, these differences may be biased by genotype-by-environment interaction.

While the breeders were encouraged to report every calf that was born, there is some concern that incomplete reporting may have affected the results for age at first calving. If a calf was deemed unworthy by the breeder, there was no obligation to report its existence to the central database. The relationship of length of productive life to age at first calving that was observed in this study corresponded with the observation of Rogers et al. (2004) wherein there was a trend for beef cows that were younger at their first parturition to have less risk of being culled than those that were older at their first calving (Figure 2). Likewise, Cushman et al. (2013) indicated that heifers that conceive earlier are more likely

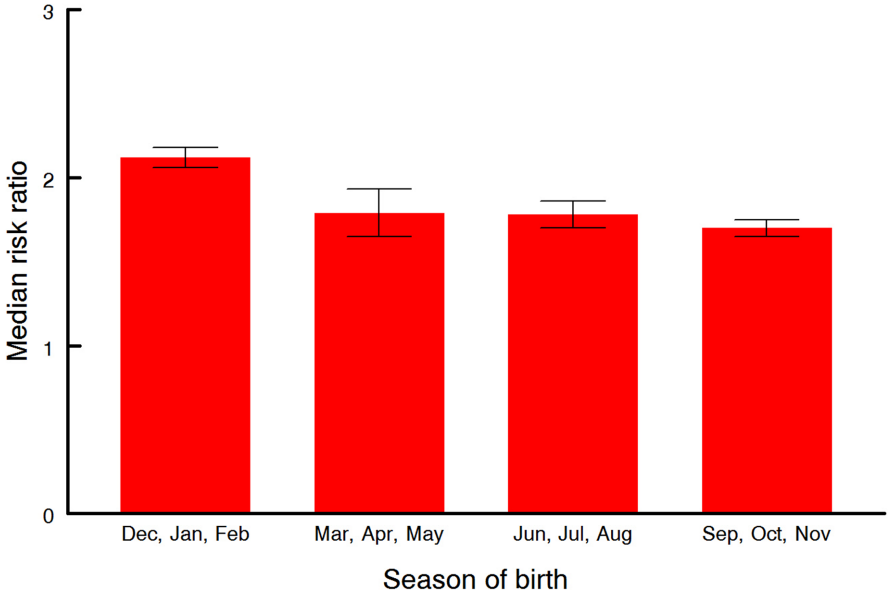

FIGURE 3 Effects of season of birth on the risk ratio indicative of longevity in Afrikaner beef cows; greater risk ratios indicate a greater likelihood of being culled and hence reduced longevity.

to remain in the productive herd longer. However, these studies and others like them from developed countries did not contemplate breeding heifers to calve first at 2 versus 3 years of age. It is also a mathematical certainty that, all other things being equal, heifers that have their first calf at a younger age will have greater length of productive life while their true longevity would be unchanged. Physical and nutritional stresses associated with calving, milk production and growth challenge the 2-year-old cow. Priorities for nutrient utilization (Short et al., 1990) indicate that reproduction is relatively unimportant for heifers calving at 2 years of age (Smith & Perry, 2015). Hence, heifers that calved at 2 years of age may be less likely to rebreed to calve as 3-year-olds due to nutrient deprivation, particularly in harsh environments. Likewise, Grobler et al. (2023) indicated that the calving percentage of Bonsmara heifers mated at 26 months was significantly higher than that of heifers mated at 14 months under extensive conditions in South Africa. Tarrés et al. (2004) observed that the optimal age for first calving to promote a long productive life was between 30 and 33 months in the Bruna dels Pirineus beef breed. Some beef producers may also choose to delay the breeding of young heifers because of the anecdotal perception that there is a higher risk of calving difficulty and potential negative consequences on lifetime performance of cows that calve at a younger age (Twomey & Cromie, 2023). They observed that cows that calved at younger ages were more likely to require assistance at their first parturition. However, Twomey and Cromie (2023) claimed that this negative consequence could be negated by good management and breeding decisions. They also found that younger calving cows weaned lighter calves for their first three lactations and themselves weighed less for their first four lactations. Hickson et al. (2010) also claimed that a considerable gain in profitability could be made by calving heifers for the first time at 2 instead of 3 years of age. In contrast, Scholtz et al. (1991) observed that Nguni heifers mated at 13–15 months of age compared to 25–27 months, weaned lighter calves throughout their productive lifetime. Finally, Núñez-Dominguez et al. (1991) found that components of lifetime productivity and economic efficiency could be improved by managing heifers to calve first at 2 years of age. Greer et al. (1980) found the probability of heifers calving first at 3 years of age being removed from the herd through 10 years of age due to physical impairment was 0.12, whereas the heifers calved first as 2-year-olds were similarly culled with a probability of 0.20. Despite evidence such as the aforementioned studies, the vast majority of Afrikaner cows in this study were calved first at around 3 years of age. This may be the result of the relatively advanced age at puberty in Afrikaner (du Plessis et al., 2006). 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 females, and 80% do not cull old cows based on their age. Culling decisions may be based, in part, on subjective factors determined by each breeder.

While fixed breeding seasons are not universally utilized in South Africa, it is recommended that cows be first exposed to bulls starting about 1.5 months after the first effective rainfall (Bergh, 2004). This is anticipated to result in females being in good body condition, and their calves being born starting about 2 months before the start of the rainy season. In these data, the vast majority of

TABLE 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 productive life
100	1.216	94	0.92	1715
99	1.159	66	0.89	1839
95	1.093	39	0.84	1984
90	1.072	31	0.81	2030
75	1.036	20	0.74	2108
50	1.008	12	0.65	2187
25	0.975	8	0.57	2243
10	0.945	6	0.51	2314
5	0.922	6	0.51	2372
1	0.871	2	0.32	2511

cows were born in the months of September–November (season 4; $N = 14{,}533$) and December–February (season 1; $N = 8929$). The observation that females born in season 1 have the least length of productive life, whereas those born in the other seasons had significantly longer productive lives suggests some asynchrony between the time of calving and fitness of the cow or her adaptation to the environment (Figure 3). It is plausible that cows whose nutritional requirements were asynchronous with the production environment are those that were born later (Funston et al., 2016), thus exposing them to greater risk of being culled. Further, cows that conceive earlier in the breeding season also calve earlier and have more time for uterine involution and to resume cycling before the next breeding season commences (Damiran et al., 2018). This resulted in heifers that calved from conception during the initial 21-day period of their first breeding season weaning approximately one more calf during their lifetime compared with heifers that conceived later (Cushman et al., 2013; Damiran et al., 2018). In addition, Afrikaner cows are noted to exhibit lactation anoestrus, causing them to have low conception rates during relatively short breeding seasons (Wells et al., 1985). Results of this study might be interpreted to suggest that shifting the breeding season earlier in the year so as to provide the cows with a better nutritional environment at the time of breeding or limiting the length of the breeding season. This change in management would provide a longer post-partum interval and could promote increased longevity of cows in the Afrikaner cattle population.

Heritability of length of productive life, as estimated from the South African Afrikaner data using the animal model, was 0.225. This estimate was similar to the value for the heritability of longevity (0.18) that was reported by Garcia et al. (2017) for Nellore cows. In these studies, culling for reproductive failure, as is the general practice in developed countries, was not evident and to some degree changes the definition of the trait being evaluated in the present study compared with much of the literature. In studies of human beings, where reproductive failure is also not a confounding factor in recording the relevant phenotype, longevity has been estimated to be between 12% and 30% heritable (Kaplanis et al., 2018; van den Berg et al., 2019). Lower estimates of the heritability for length of productive life or longevity are more frequently reported in studies where culling for reproductive failure was more commonplace: 0.08 (Larracharte et al., 2021), 0.11 (Mészáros, Kadlečík, et al., 2013), 0.05 (MacNeil & Vukasinovic, 2011), 0.14 (Rogers et al., 2004) and 0.037 (Brzáková et al., 2019). Price and Schluter (1991) postulated that the low heritability of life-history traits, including longevity, resulted from them being subjected to greater environmental variation than metric traits with higher heritability rather than a lack of additive genetic variance. Supporting this line of reasoning, Brzáková et al. (2019) concluded that heritability for longevity appears to be low, but additive genetic variance is likely to be sufficient to identify animals with high genetic merit. In the present data, the genetic standard deviation of the risk ratio was approximately 0.52. In addition, approximately 25% of the sires recorded in the original data set had records that were not censored from two or fewer daughters. This would seemly reflect either very low cow-to-bull ratios being used in practice or errors in the recorded parentage. South African stud breeders were previously found to misidentify 10.0% and 17.2% of sire-progeny pairs in Bonsmara and Drakensberger respectively (Sanarana, 2022). Thus, it was hypothesized that removing the small paternal half-sib families from the data set would reduce the frequency of misidentified sires. Misidentification of sires has been previously reported to severely bias estimates of genetic parameters towards zero (Charmantier & Réale, 2005; Senneke et al., 2004). Bot Steffl (2023) analysed longevity, defined as the difference between the birth date of a cow and the date at which she gave birth to her last reported calf, with these data but without restricting the size of paternal half-sib families and an estimate of heritability of 0.083 was obtained.

Presented in Table 1 are summary statistics characterizing the pool of Afrikaner sires for their EBV, the distribution of number of uncensored daughters in the data, the accuracy of the sire breeding values and the expected length of productive life for the daughters of the sires. Risk ratios for the 5th and 95th percentiles ranged from 0.922 to 1.093, indicating that the risk of culling daughters from the best sires was approximately 84% of the risk of culling daughters from the worst sires. The inter-quartile range of 135 days in projected length of productive life provides some reflection on the opportunities available to breeders from selection for this trait. Selection pressure will need to be sustained across several generations in order to make meaningful progress in increasing the length of productive life. Implementation of a selection program to improve longevity will be challenging. First, generating uncensored observations requires animals to live their full life, which prolongs the generation interval. Most, if not all, selection decisions will be made before the trait can be observed on any candidate for selection. Second, the heritability of length of productive life implies the accuracy of an EBV for a candidate for selection based on its own phenotype will have limited accuracy. Increasing the accuracy of an EBV to a reasonable level will require the production of many progeny or a reasonably accurate genomic breeding value. Developing a useful genomic EBV is likely to be challenging but should be investigated.

Environmental trends in longevity of Afrikaner cattle indicate large inter-annual fluctuations. These effects may be explained, in part, by the reduced number of herds over the period of years covered by this research. There were 215 distinct herds identified in the first 3 years of data that were used in this study, as compared to there being only 30 distinct herds identified in the last 3 years of data. These liquidations would disproportionately affect young animals. The lack of recording of reasons for disposal, as recommended by the International Committee for Animal Recording (2018), negated the opportunity to classify the animals in these herds as being at either the end of their productive life or as being censored.

Genetic trend in the risk ratio for length of productive life was essentially flat for cows born from 1980 until approximately 2008 (Figure 4). Cows born after 2008 appeared to have increasing risk for genetically reduced length of productive life. The relatively recent observed trend in length of productive life may be the result of an increased propensity of breeders of cull open cows and/or recent herd dispersions. In the only other report for genetic trend for longevity in beef cattle, Larracharte et al. (2021) found the breeding value for length of productive life increased by 0.0004 days/year for Uruguayan Angus. These estimates of genetic trend may be ramifications of both

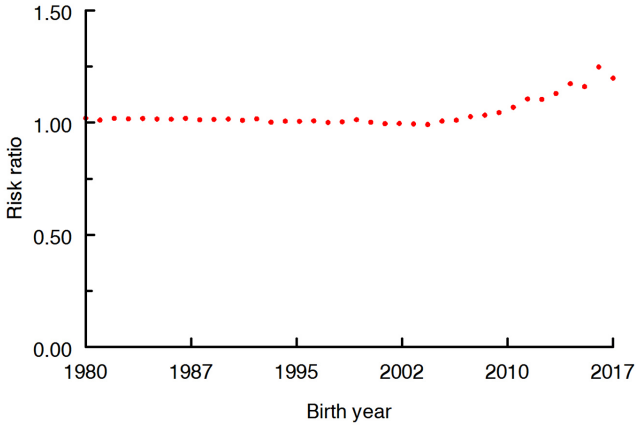

FIGURE 4 Genetic trend in the risk ratios indicative of length of productive life of Afrikaner beef cows; greater risk ratios indicate a shorter interval between the first and last calves born to a cow.

the heritability of longevity and the lack of any meaningful selection differential having been achieved in a genetic improvement program, despite longevity being an economically relevant trait.

Use of time-dependent covariates to model changes in herd composition and environment over time would also potentially be valuable (Gröhn et al., 1997). MacNeil and Vukasinovic (2011), among others, made effective use of time-dependent covariates in conducting a prototype genetic evaluation for sustained reproductive success in data where breeding seasons and culling of non-pregnant cows occurred on an annual basis. However, in the present data, at least in some of the herds, Afrikaner breeders allowed the bulls to remain with the cows year-round and there was very limited culling of cows based on any defined criterion or at a fixed point in time. A random time-dependent covariate could be arbitrarily defined at a cost of greatly increasing the number of elemental records (Jovanovac et al., 2013). It should further be noted that the statistical methodology that was used in this study proved to be computationally demanding. Van Melis et al. (2010) made a similar observation relative to including survival in proportional hazard models. Given the economic value of longevity, more attention should focus on issues in computation of breeding values for this trait and early-in-life predictors of it (Forabosco et al., 2006); a recommendation with which we concur.

4 | CONCLUSIONS

These data suggest cows that are older when they first calve have a shorter length of productive life. Shifting the breeding season to start slightly earlier in the year to provide the cows with a better nutritional environment at the time of breeding or limiting the length of the breeding

season so as to provide a longer post-partum interval might promote increased longevity. The moderate estimate of heritability for length of productive life indicates the potential to make genetic improvement in this trait. In these data, genetic potential for length of productive life has been compromised in more recent years relative to what it was in years prior.

AUTHOR CONTRIBUTIONS

MDM and MMS conceived the study. AMBS conducted preliminary analyses of the data and wrote an initial draft of the manuscript that was extensively revised with inputs from all of the authors. MMS provided expert insights into the Afrikaner breed. LPS, MDM and TP conducted the final survival analysis, and MDM and MGG supervised the research.

ACKNOWLEDGEMENTS

We thank the Afrikaner Breeders' Society for allowing access to the data that was used in this study. The South Dakota Agricultural Experiment Station provided funding to support this Master's degree study of Ms. Bot Steffl.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest relative to the conduct of this research or the content of this article.

FUNDING INFORMATION

The South Dakota Agricultural Experiment Station provided funding to support this Master's degree study of Ms. Bot Steffl.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Afrikaner Breeders Society. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the author(s) with the permission of Afrikaner Breeders Society.

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REFERENCES

Basarab, J. A., Crowley, J. J., Abo-Ismail, M. K., Manafiazar, G. M., Akanno, E. C., Baron, V. S., & Plastow, G. (2018). Genomic retained heterosis effects on fertility and lifetime productivity in beef heifers. *Canadian Journal of Animal Science*, *98*(4), 642–655. https://doi.org/10.1139/cjas-2017-0192

Bergh, L. (2004). Breeding seasons for beef cattle in South Africa. *SA-Animal Science*, *5*, 11–17. https://www.sasas.co.za/wp-content/uploads/2012/10/Bergh2004PopSci_0.pdf

Bot Steffl, A. M. (2023). Afrikaner longevity: A survival analysis. MS thesis, South Dakota State University, Brookings. 82 pages.

Brzáková, M., Svitáková, A., Čítek, J., Veselá, Z., & Vostrý, L. (2019). Genetic parameters of longevity for improving profitability of beef cattle. *Journal of Animal Science*, *97*(1), 19–28. https://doi.org/10.1093/jas/sky390

Charmantier, A., & Réale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild? *Molecular Ecology*, *14*, 2839–2850. https://doi.org/10.1111/j.1365-294X.2005.02619.x

Clark, T., Bradburn, M., Love, S., & Altman, D. G. (2003). Survival analysis part I: Basic concepts and first analyses. *British Journal of Cancer*, *89*, 232–238. https://doi.org/10.1038/sj.bjc.6601118

Cushman, R. A., Kill, L. K., Funston, R. N., Mousel, E. M., & Perry, G. A. (2013). Heifer calving date positively influences calf weaning weights through six parturitions. *Journal of Animal Science*, *91*, 4486–4491.

Dákay, I., Márton, D., Bene, S., Kiss, B., Zsuppán, Z., & Szabó, G. (2006). The age at first calving and the longevity of beef cows in Hungary. *Archiv für Tierzucht Dummerstorf*, *49*(5), 417–425.

Damiran, D., Larson, K. A., Pearce, L. T., Erickson, N. E., & Lardner, B. H. A. (2018). Effect of calving period on beef cow longevity and lifetime productivity in western Canada. *Translational Animal Science*, *2*(suppl 1), S61–S65. https://doi.org/10.1093/tas/txy020

du Plessis, I., Hoffman, L. C., & Calitz, F. J. (2006). Influence of reproduction traits and pre-weaning growth rate on herd efficiency of different beef breed types in an arid sub-tropical environment. *South African Journal of Animal Science*, *36*(2), 89–98.

Ducrocq, V. (1997). Survival analysis, a statistical tool for longevity data. In: Proceedings of the 48th Annual Meeting of the European Association for Animal Production, 25–28 August 1997, Vienna, Austria.

Forabosco, F., Boettcher, P., Bozzi, R., Filippini, F., & Bijma, P. (2006). Genetic selection strategies to improve longevity in Chianina beef cattle. *Italian Journal of Animal Science*, *5*, 117–127.

Funston, R. N., Grings, E. E., Roberts, A. J., & Tibbitts, B. T. (2016). Invited review: Choosing a calving date. *The Professional Animal Scientist*, *32*(2), 145–153. https://doi.org/10.15232/pas.2015-01463

Garcia, D. A., Rosa, G. J. M., Valente, B. D., Carvalheiro, R., Fernandes Júnior, G. A., & Albuquerque, L. G. (2017). Evaluation of longevity modeling censored records in Nellore. *Animal*, *11*(12), 2113–2119. https://doi.org/10.1017/S1751731117001136

Garcia, J., Anderson, D., Herring, A., & Riley, D. (2015). Economic analysis of selecting for cow longevity. https://ageconsearch.umn.edu/record/196863. Proc. Southern Agric. Econ. Assoc. 2015 Annual Meeting, January 31–February 3, Atlanta, Georgia.

Golden, B. L., Garrick, D. J., & Benyshek, L. L. (2009). Milestones in beef cattle genetic evaluation. *Journal of Animal Science*, *87*, E3–E10. https://doi.org/10.2527/jas.2008-1430

Greer, R. C., Whitman, R. W., & Woodward, R. R. (1980). Estimation of probability of beef cows being culled and calculation of expected herd life. *Journal of Animal Science*, *51*(1), 10–19.

Grobler, S. M., Scholtz, M. M., Neser, F. W. C., Morey, L., & Greyling, J. P. (2023). Reproductive performance of extensively managed beef heifers mated at 14 or 26 months in the central bushveld bioregion. *South African Journal of Agricultural Extension*, *51*(1), 155–165.

Gröhn, Y. T., Ducrocq, V., & Hertl, J. A. (1997). Modeling the effect of a disease on culling: An illustration of the use of time-dependent covariates for survival analysis. *Journal of Dairy Science*, *80*, 1755–1766. https://doi.org/10.3168/jds.S0022-0302(97)76109-5

Hickson, R. E., Lopez-Villalobos, N., Kenyon, P. R., Ridler, J., & Morris, S. T. (2010). Profitability of calving heifers at 2 compared with 3 years of age and the effect of incidence of assistance at parturition on profitability. *Animal Production Science*, *50*(6), 354–358. https://doi.org/10.1071/AN09180

International Committee for Animal Recording. (2018). Section 3 – ICAR guidelines for beef cattle production recording. https://www.icar.org/index.php/icar-recording-guidelines/

Jovanovac, S., Raguž, N., Sölkner, J., & Mészáros, G. (2013). Genetic evaluation for longevity of Croatian Simmental bulls using a piecewise Weibull model. *Archiv fur Tierzucht*, *56*(9), 89–101. https://doi.org/10.7482/0003-9438-56-009

Kaplan, E. L., & Meier, P. (1958). Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, *53*(282), 457–481. https://doi.org/10.2307/2281868

Kaplanis, J., Gordon, A., Shor, T., Weissbrod, O., Geiger, D., Wahl, M., Gershovits, M., Markus, B., Sheikh, M., Gymrek, M., Bhatia, G., MacArthur, D. G., Price, A. L., & Erlich, Y. (2018). Quantitative analysis of population-scale family trees with millions of relatives. *Science*, *360*(6385), 171–175. https://doi.org/10.1126/science.aam9309

Larracharte, A., Espasandin, A. C., & Urioste, J. I. (2021). Longevity and reproductive traits in Angus cattle: Genetic parameters, predicted and realized genetic change. *Livestock Science*, *250*, 104604. https://doi.org/10.1016/j.livsci.2021.104604

López de Maturana, E., Ugarte, E., & González-Recio, O. (2007). Impact of calving ease on functional longevity and herd amortization costs in Basque Holsteins using survival analysis. *Journal of Dairy Science*, *90*, 4451–4457. https://doi.org/10.3168/jds.2006-734

MacNeil, M. D., & Vukasinovic, N. (2011). A prototype national cattle evaluation for sustained reproductive success in Hereford cattle. *Journal of Animal Science*, *89*(6), 1712–1718. https://doi.org/10.2527/jas.2010-3353

Makina, S. O., Muchadeyi, F. C., van Marle-Köster, E., Taylor, J. F., Makgahlela, M. L., & Maiwashe, A. (2015). Genome-wide scan for selection signatures in six cattle breeds in South Africa. *Genetics, Selection, Evolution*, *47*, 92. https://doi.org/10.1186/s12711-015-0173-x

McIntosh, M. M., Spiegal, S. A., McIntosh, S. Z., Sanchez, J. C., Estell, R. E., Steele, C. M., Elias, E. H., Bailey, D. W., Brown, J. R., & Cibils, A. F. (2023). Matching beef cattle breeds to the environment for desired outcomes in a changing climate: A systematic review. *Journal of Arid Environments*, *211*, 104905. https://doi.org/10.1016/j.jaridenv.2022.104905

Mészáros, G., Kadlečík, O., Kasarda, R., & Sölkner, J. (2013). Analysis of longevity in the Slovak Pinzgau population – Extension to the animal model. *Czech Journal of Animal Science*, *58*(7), 289–295. https://www.agriculturejournals.cz/pdfs/cjs/2013/07/01.pdf

Mészáros, G., Sölkner, J., & Ducrocq, V. (2013). The survival kit: Software to analyze survival data including possibly correlated random effects. *Computer Methods and Programs in Biomedicine*, *110*(3), 503–510. https://doi.org/10.1016/j.cmpb.2013.01.010

Morales, R., Phocas, F., Solé, M., Demyda-Peyrás, S., Menéndez-Buxadera, A., & Molina, A. (2017). Breeding beef cattle for an extended productive life: Evaluation of selection criteria in the Retinta breed. *Livestock Science*, *204*, 115–121. https://doi.org/10.1016/j.livsci.2017.08.014

Nkadimeng, M., van Marle-Köster, E., Nengovhela, N., & Makgahlela, M. (2022). Understanding beef cattle production practices and associated factors constraining performance: A survey of smallholder farmers in South Africa. *The Journal of Agriculture and Rural Development in the Tropics and Subtropics*, *123*(1), 131–145. https://doi.org/10.17170/kobra-202204216054

Núñez-Dominguez, R., Cundiff, L. V., Dickerson, G. E., Gregory, K. E., & Koch, R. M. (1985). Effects of heterosis on longevity in beef cattle. Beef research program progress report. *USDA Agricultural Research Service, Clay Center, Nebraska USA*, *2*, 10–12.

Núñez-Dominguez, R., Cundiff, L. V., Dickerson, G. E., Gregory, K. E., & Koch, R. M. (1991). Lifetime production of beef heifers calving first at two vs three years of age. *Journal of Animal Science*, *69*(9), 3467–3479. https://doi.org/10.2527/1991.6993467x

Olechnowicz, J., Kneblewski, P., Jaśkowski, J. M., & Włodarek, J. (2016). Effect of selected factors on longevity in cattle: A review. *The Journal of Animal and Plant Sciences*, *26*, 1533–1541.

Pienaar, L., Grobler, J. P., Scholtz, M. M., Swart, H., Ehlers, K., Marx, M., MacNeil, M. D., & Neser, F. W. C. (2018). Genetic diversity of Afrikaner cattle in southern Africa. *Tropical Animal Health and Production*, *50*(2), 399–404. https://doi.org/10.1007/s11250-017-1447-9

Price, T., & Schluter, D. (1991). On the low heritability of life history traits. *Evolution*, *45*(4), 853–861.

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rogers, P., Gaskins, C., Johnson, K. A., & MacNeil, M. (2004). Evaluating longevity of composite beef females using survival analysis techniques. *Journal of Animal Science*, *82*, 860–866. https://doi.org/10.2527/2004.823860x

Rohrer, G. A., Baker, J. F., Long, C. R., & Cartwright, T. C. (1988). Productive longevity of first-cross cows produced in a five-breed diallel: II. Heterosis and general combining ability. *Journal of Animal Science*, *66*(11), 2836–2841. https://doi.org/10.2527/jas1988.66112836x

Sanarana, Y. P. (2022). Genome-wide scan of single nucleotide polymorphisms for parentage analyses in South African indigenous beef breeds. PhD thesis, University of Pretoria, South Africa. 109 pages.

Scholtz, M. M., Lombard, P. E., & Enslin, C. B. (1991). A note on the early calving of beef heifers. *South African Journal of Animal Science*, *21*(4), 206–209.

Scholtz, M. M., Neser, F. W. C., & Mamabolo, J. (2016). The role of the Afrikaner in the development of composite breeds in South Africa. In M. M. Scholtz, F. W. C. Neser, & L. Tissier (Eds.), *The Afrikaner breed of cattle: South Africa's heritage for food security* (pp. 18–21). Agricultural Research Council.

Senneke, S. L., MacNeil, M. D., & Van Vleck, L. D. (2004). Effects of sire misidentification on estimates of genetic parameters for birth and weaning weights in Hereford cattle. *Journal of Animal Science*, *82*(8), 2307–2312. https://doi.org/10.2527/2004.8282307x

Short, R. E., Bellows, R. A., Staigmiller, R. B., Berardinelli, J. G., & Custer, E. E. (1990). Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. *Journal of Animal Science*, *68*, 799–816.

Smith, M. F., & Perry, G. (2015). Managing reproduction in postpartum cows. Chapter 31, iGrow Beef: Best Management Practices for Cow-Calf Production. South Dakota State University, College of Agriculture and Biological Sciences, SDSU Extension, Brookings, South Dakota (pp. 352–360).

Steenkamp, J. J., & Tissier, L. (2016). The history of the Afrikaner cattle Breeders' Society. In M. M. Scholtz, F. W. C. Neser, & L. Tissier (Eds.), *The Afrikaner breed of cattle: South Africa's heritage for food security* (pp. 10–17). Agricultural Research Council.

Szabó, F., & Dákay, I. (2009). Estimation of some productive and reproductive effects on longevity of beef cows using survival analysis. *Livestock Science*, *122*(2–3), 271–275. https://doi.org/10.1016/j.livsci.2008.09.024

Tarrés, J., Puig, P., Ducrocq, V., & Piedrafita, J. (2004). Factors influencing the length of productive life and replacement rates in the Bruna dels Pirineus beef breed. *Animal Science*, *78*, 13–22.

Twomey, A. J., & Cromie, A. R. (2023). Impact of age at first calving on performance traits in Irish beef herds. *Journal of Animal Science*, *101*. https://doi.org/10.1093/jas/skad008

van den Berg, N., Rodríguez-Girondo, M., van Dijk, I. K., Mourits, R. J., Mandemakers, K., Janssens, A. A. P. O., Beekman, M., Smith, K. R., & Slagboom, P. E. (2019). Longevity defined as top 10% survivors and beyond is transmitted as a quantitative genetic trait. *Nature Communications*, *10*, 35. https://doi.org/10.1038/s41467-018-07925-0

Van Melis, M. H., Eler, J. P., Oliveira, H. N., Rosa, G. J. M., Silva, J. A. V., Ferraz, J. B. S., & Pereira, E. (2007). Study of stayability in Nellore cows using a threshold model. *Journal of Animal Science*, *85*, 1780–1786.

Van Melis, M. H., Oliveira, H. N., Eleer, J. P., Ferraz, J. B. S., Casellas, J., & Varona, L. (2010). Additive genetic relationship of longevity with fertility and production traits in Nellore cattle based on bivariate models. *Genetics and Molecular Research*, *9*(1), 176–187.

Vukasinovic, N. (1999). Application of survival analysis in breeding for longevity. In: Proc. 4th International Workshop on genetic improvement of functional traits in cattle, Jouy-en-Josas, France. Interbull Bulletin 21, 3–10.

Wellnitz, K. R., Parsons, C. T., Dafoe, J. M., Boss, D. L., Wyffels, S. A., DelCurto, T., & Van Emon, M. L. (2022). Impacts of dam age on lifetime productivity of Angus replacement beef females. *Animals (Basel)*, *12*(20), 2768. https://doi.org/10.3390/ani12202768

Wells, P. L., Holness, D. H., Freymark, P. J., McCabe, C. T., & Lishman, A. W. (1985). Fertility in the Afrikaner cow. 2. Ovarian recovery and conception in suckled and non-suckled cows post partum. *Animal Reproduction Science*, *8*(4), 315–326. https://doi.org/10.1016/0378-4320(85)90047-8

Yazdi, M. H., Visscher, P. M., Ducrocq, V., & Thompson, R. (2002). Heritability, reliability of genetic evaluations and response to selection in proportional hazard models. *Journal of Dairy Science*, *85*(6), 1563–1577. https://doi.org/10.3168/jds.S0022-0302(02)74226-4

How to cite this article: Bot Steffl, A. M., MacNeil, M. D., Scholtz, M. M., Sanglard, L. P., Passafaro, T., & Gonda, M. G. (2024). Longevity in South African Afrikaner cows as assessed through survival analysis. *Journal of Animal Breeding and Genetics*, *00*, 1–10. https://doi.org/10.1111/jbg.12847