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Short communication

The effect of the Afrikaner infusion project on longevity: A survival analysis

A.M. Bot Steffl [a], M.G. Gonda [a], M.M. Scholtz [b,c], M.D. MacNeil [b,c,d,*]

[a] Department of Animal Science, South Dakota State University, Brookings, SD, United States of America
[b] Agricultural Research Council, Animal Production Institute, Irene, South Africa
[c] Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein, South Africa
[d] Delta G, Miles City, Montana, United States of America

HIGHLIGHTS

- Infusion of Bonsmara into Afrikaner immediately increased length of life.
- Effects of infusion of Bonsmara into Afrikaner dissipated as backcrossing progressed.
- Alternative strategies may be needed to increase length of life.

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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 the 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.

1. 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), Huguenoot (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

* Corresponding author.
E-mail address: macneil.deltag@gmail.com (M.D. MacNeil).

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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.

2. Materials and methods

Data that pertained to the Afrikaner breed and recorded in the Integrated Registration and Genetic Information System (INTERGIS) (https://www.gov.za/agriculture-national-animal-recording-and-improvement-scheme) were available for 74,402 cows that had produced 269,457 calves. 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 2544 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 Schoenfled (1982) residuals and were subsequetially analyzed using the Survival Kit V.6.1 interface for R (Mészáros et al., 2013). Hazards (β_i) ± 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:

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

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}):

$$\text{RHV} = 1 - \left(\sum_{i}^{n} P_{si} \text{ x } P_{di}\right)$$

where *n* is the number of breeds and breed types (4) (Falconer and 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%).

3. 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 and 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 and 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 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 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 (1095 days; Fig. 1). However, this result

Table 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	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.

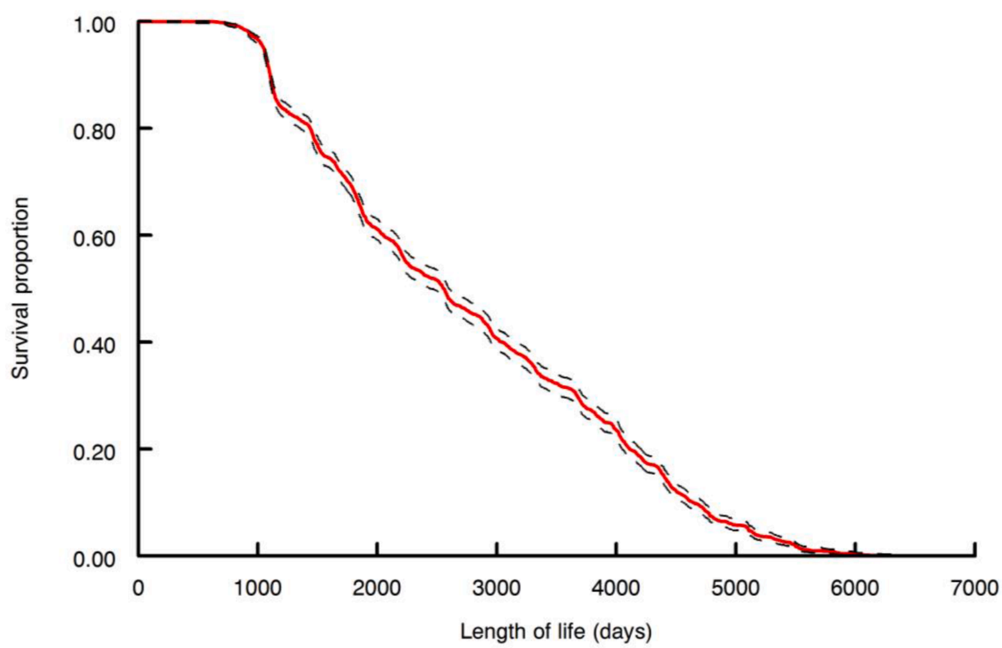

Fig. 1. Kaplan-Meier survivor curve (solid red line) and 95% confidence interval (dashed black lines) for cows included in the Afrikaner infusion project based on the interval from the birthdate of the cow to the birthdate of her last recorded calf.

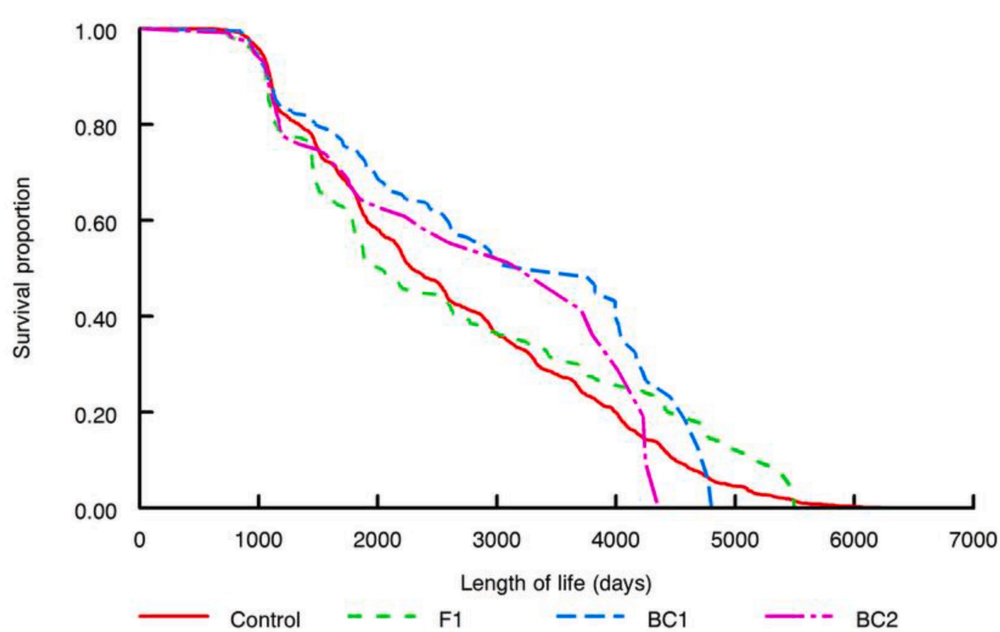

Fig. 2. . Kaplan-Meier survivor curves of for Bonsmara x Afrikaner (F1), Afrikaner x F1 (BC1), and Afrikaner x BC1 (BC2) cows in the different generations of the infusion project based on the interval from the birthdate of the cow to the birthdate of her last recorded calf.

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 3837 days for the controls, 4211 days for the F1, 4457 days for the BC1 and 4299 days for BC2 (Fig. 2). The Kaplan-Meier curves differed by generation of the infusion project (Log-rank $\chi^2 = 23.8$, $P < .001$). 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. Tshipulisoet al. (2008) demonstrated such effects on breed composition in backcrossing genes from L1 Hereford into the genetic background of a 3-breed composite beef population. 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 and 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).

The data used for this study arose from reports submitted by breeders rather than from a designed experiment. Afrikaner breeders may not always objectively make selection and culling decisions based on breeding values or performance records. 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% of replacement heifers were reported as open after their first breeding season. The survey also indicated that 53% of the farmers do not cull non-productive animals 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 and 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.

4. 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 towards the purebred Afrikaners suggesting continued generations of backcrossing might not be effective for maintaining the short-term gains in longevity.

CRediT authorship contribution statement

A.M. Bot Steffl: Writing – original draft, Investigation, Formal analysis. **M.G. Gonda:** Supervision, Writing – review & editing, Funding acquisition. **M.M. Scholtz:** Conceptualization, Writing – review & editing. **M.D. MacNeil:** Conceptualization, Data curation, Formal analysis, Writing – review & editing, Project administration.

Declaration of Competing Interest

The authors have no competing interests

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