GENETIC ANALYSIS OF LONGEVITY AND PERFORMANCE TRAITS OF SAHIWAL CATTLE IN KENYA

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DECLARATION AND RECOMMENDATION

Declaration

I declare that this research thesis is my original work and to the best of my knowledge, has not, wholly or in part, been submitted for an award of a degree in any other institution.

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Recommendation

This proposal has been submitted to the Post-Graduate school for examination with our approval as University Supervisors.

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ABSTRACT

Genetic and phenotypic parameters for longevity, genetic relationship between longevity and growth, milk yield and fertility traits and rate of inbreeding were estimated for Sahiwal cattle in Kenya. The aim was to assess the genetic diversity and inbreeding depression for performance traits. Data utilized were for cows born between 1972 and 2004 and with milk production records between 1976 and 2008. Measures of longevity related to productive life were: time between birth (Long_1) or first calving (Long_2) and last milking record in days, number of lactations initiated (Long_3), total number of days in lactation over all lactations (Long_4) and total milk yield over all lactations (kg) (Long_5). Measures of longevity related to survival were defined as survival from birth to 44 months (Long6_44), 56 months (Long6_56), 80 months (Long6_80), 92 months (Long6_92), 104 months (Long6_104), and 128 months (Long6_128). Longevity was also defined as survival from first calving as survival from for 12 months (Long7_12), 36 (Long7_36), 60 (Long7_60), 84 (long7_84) and 96 months (Long7_96) from first calving. Longevity measures related to productive life were analysed using linear models while those related to survival were analysed using threshold models. Effects of inbreeding on the traits were determined by fitting four regression models (linear, quadratic, exponential and Michaelis-Menten) to the errors generated by the animal model. Estimates of heritability for longevity measures related to survival were higher (0.084±0.053 to 0.119±0.035) compared to those of measures related to productive life (0.038±0.032 to 0.097±0.04). Comparatively, survival from first calving to predefined ages had higher heritability estimated (0.090 to 0.119) compared to survival from birth (0.084 to 0.104). Long7_96 had the highest additive genetic variance and heritability estimate, and therefore should be used for genetic evaluation of longevity in Sahiwal cattle in Kenya. Genetic correlations between measures of longevity and first lactation milk yield and fertility were positive (0.41 to 0.99) and negative (-0.02 to -0.85), respectively. First lactation milk yield had the highest genetic correlation and should be used as a selection criterion for longevity. Michaelis-Menten model had the highest significant (P < 0.001) for all the traits studied. Inbreeding shortened calving interval and age at first calving and increasing lactation length. Inbreeding depression was greater after 15% inbreeding. Genetic evaluation of the Kenyan Sahiwal should account for inbreeding. This study has also provided genetic and phenotypic parameters to enable inclusion of longevity in the breeding objective for the Sahiwal cattle improvement programme

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CHIAPTER ONE
INTRODUCTION

1.1   Background information

Longevity or the age at which a cow leaves the breeding herd is a trait of great economic importance in dairy and beef cattle breeding (Banga *et al.,* 2013). Productive longevity can also be described as the number of calvings per female (Varona *et al.,* 2012). In beef and dairy cattle, longevity plays a considerable role in the farm economy by increasing the profit realised per cow and enables greater response to selection because fewer animals exit the herd due to involuntary culling (Garcia *et al.,*2015), a situation that provides greater for selection intensity among females, and surplus heifers for sale (Banga *et al.,* 2013).

Although milk production is considered as the single most important trait in dairy farming, cattle breeding programmes are changing their breeding objectives to include longevity and other traits (type and functional) (Banga *et al.,* 2013: 2014), so that cows can meet the challenges associated with high milk production. Direct selection for longevity results in improved health and fitness (Garcia *et al.,* 2015) and even milk production of cows (Kern *et al.,* 2014a). Longevity is also associated with decreased cases of involuntary culling due to reproduction, udder health and workability (Kern *et al.,* 2015). Decrease in involuntary culling is accompanied by an increase in voluntary culling due to low production. Therefore, breeding for longevity is considered to have ethical and economic benefits since it results in favourable response in profitability of beef and dairy cattle enterprises (Garcia *et al.,* 2015). However, inclusion of longevity in the breeding objective is hampered because the trait is lowly heritable (Kern *et al.,* 2014a; Van Pelt *et al.,* 2015). Estimates of heritability for longevity defined variously based on the length of time interval for survival after first calving range from 0.002 to 0.031 (Van Pelt *et al.,* 2015). When defined as total milk production over all lactations, number of lactations initiated, total number of days in lactation over all lactations, time between birth and last milk recording in months; and time from first calving to last milk recording in months, the estimates ranged from 0.05 to 0.18 (Kern *et al.,* 2014b). Thus, heritability estimates for longevity regardless of how the trait is defined or analysed are low, implying that direct selection may not yield significant gains (Kern *et al.,* 2014b).

Another limitation of selecting directly for longevity is the delay in availability of phenotypic information (Lagrota *et al.,* 2010), which may lead to increase in generation interval (Melo *et*

al., 2014). The age at exit from a herd has been reported to be around 80 months from birth or 54 months from first calving (Kern *et al.,* 2014c), delaying the time in which information on exit from the herd is obtained. Information on other measures of longevity such as lifetime milk production, number of lactations initiated, total days in milk is also available once a cow exits the herd. Availability of traits expressed early in life and which are favourably correlated to longevity can be useful in selecting for this trait. Genetic correlations between longevity and linear and fertility traits have been reported to be low to moderately positive (Zavadilová *et al.,* 2009b; Van Melis *et al.,* 2010; Kern *et al.,* 2014a). Such traits can be used in breeding programmes to indirectly select for longevity early in an animal's life, leading to improvement in longevity and reduction in generation interval.

Reproductive performance is a crucial component of culling criteria and therefore influences longevity in cattle herds and is regarded as the single most economically important trait in cattle (Sewalem *et al.,* 2008). Poor reproductive performance leads to increased involuntary culling, fewer lactations initiated and calves born and less milk in a cow's lifetime, as well as increased cost of replacement. Therefore, since productive longevity is closely related to fertility, it is important to consider the genetic effects of both traits simultaneously. Other traits which influence culling decisions such as body conformation type traits have also been considered as proxy for longevity (Kern *et al.,* 2014a, 2017). Despite its importance in cattle, longevity has not been studied in the Sahiwal cattle and has not been recommended for inclusion in the breed's breeding objective (Roessler *et al.,* 2010; Ilatsia *et al.,* 2011; Ilatsia *et al.,* 2012).

Since direct selection for longevity is not feasible partly due to delay in acquisition of data, correlated response due to selection on traits that are genetically correlated with longevity should be explored. Favorable associations between longevity and linear type traits have been reported, indicating selecting for these traits would improve longevity (Kern *et al.,* 2014a). Based on phenotypic relationships, Kern *et al.* (2017) found that type traits were not a good indirect indicator for productive life. However, there seems to be an important influence of the definition of longevity on the associations reported (Kern *et al.,* 2014a). Fertility traits such as number of services per conception, difficulties in calving, days open and other fertility traits were reported to influence longevity significantly (Sewalem *et al.,* 2008). Estimates of genetic correlations between longevity and other performance traits, which can be used as selection criteria for longevity in the Sahiwal breed in Kenya are lacking.

Whereas the current quest is to improve longevity, the trait and other correlated traits are negatively affected by inbreeding in livestock populations. Longevity and reproductive performance have been shown to decrease while, rate of disposal or loss of replacement heifers before first calving, age at puberty increased due to inbreeding through reduced growth (du Toit *et al.,* 2012). Studies of inbreeding depression on longevity are rare. However, for every increase of 1% in inbreeding, productive life has been reported to decrease by about 13 days according to the Canadian Dairy Network (CDN, 2008). Cows with high inbreeding level have also been reported to have a higher risk of being culled (Rokouei *et al.,* 2010). Effects of inbreeding on non-production traits include decreased reproductive efficiency and decreased stayability. The negative effects on traits related to fitness have been attributed to reduced heterozygosity as inbreeding accumulates (Falconer and Mackay, 1996).

Inbreeding level and rate of inbreeding in the Sahiwal cattle population in Kenya has been found to be on an upward trend and is above 1% (Mwangi *et al.,* 2016). It is therefore expected that there will be depression in production and functional traits such as fertility and longevity. Inbreeding depression depends not only on actual level of inbreeding but also on the rate of inbreeding. At a slow rate of inbreeding per generation, natural selection counteracts the effects of inbreeding by removing the less adapted inbred animal (Van Wyk *et al.,* 2009). Therefore, animals with the same level of inbreeding may have different inbreeding depression effects depending on the completeness of their respective pedigrees (González-Recio *et al.,* 2007; Gutiérrez *et al.,* 2009). The quality of pedigree can be accounted for by estimating the rate of inbreeding (Gonzalez-Recio *et al.,* 2007). Estimated this way, the estimated coefficient corrects for depth of the pedigree depth of an individual and indicates the increment in inbreeding regardless of number of known generations in its pedigree (Gonzalez-Recio *et al.,* 2007).

1.2   Statement of the problem

Inclusion of longevity in breeding objective of cattle is hampered by the delayed availability of phenotypic information. Genetic correlations between longevity and traits expressed early in an animals' life which can be useful in selecting for longevity have not been estimated. Further, though inbreeding levels for Kenyan Sahiwal breed have been on an upward trend due to selection in a closed nucleus with a small effective population size, inbreeding

depression for longevity and fertility traits in the Sahiwal population in Kenya has not been assessed. Consequently, the long-term sustainability of the Sahiwal breeding programme is threatened due to reduced viability of the population and variance of genetic gains across generations.

1.3   Objectives of the study

The overall goal of this study was to contribute to increased contribution of the Sahiwal cattle to livestock farmers' income through increased genetic improvement of longevity and performance traits.

The specific objectives were

i.   To determine variance components, genetic and phenotypic parameters for longevity for Sahiwal cattle in Kenya

ii.   To evaluate the genetic relationship between longevity and milk yield and fertility traits in Sahiwal cattle in Kenya

iii. To determine the effect of inbreeding on longevity, first lactation milk yield and fertility traits in Sahiwal cattle in Kenya

1.4   Research questions

i.   What are the variance components, genetic and phenotypic parameters for longevity in the Sahiwal cattle in Kenya?

ii.   What is the genetic relationship between longevity and milk yield and fertility traits in Sahiwal cattle Kenya?

iii. What is the effect of inbreeding on longevity, first lactation milk yield and fertility traits in Sahiwal cattle in Kenya?

1.5   Justification of the study

Estimation of genetic and phenotypic parameters and genetic correlations between longevity and traits expressed early in an animal's life will provide a possibility of inclusion of longevity in the selection criteria and breeding goal of the Kenyan Sahiwal population. This will lead to genetic improvement of longevity without lengthening generation intervals. Assessing inbreeding depression on performance traits and longevity will form the basis of

countering the negative effects of inbreeding on fitness and reduced performance thereby improving viability of the Sahiwal population in Kenya.

CHAPTER TWO
LITERATURE REVIEW

2.1   Introduction

Sahiwal are humped zebu cattle that originated from India and Pakistan. The breed was imported into Kenya between 1939 and 1963 to improve the performance of the local East African zebu (Muhuyi, 1997). The founding population consisted of 60 bulls and 20 cows which were introduced in Livestock Improvement Centres (LICs) across the country. After some basic performance evaluation, the best animals from the LICs were taken to Naivasha to establish the National Sahiwal Stud (NSS) in 1963. Breeding of this population followed a closed nucleus after the recommendation by Meyn and Wilkins (1974) for genetic improvement of milk and growth rate. To date breeding of the Sahiwal has been under a closed nucleus breeding programme except for the introduction of semen from Pakistan in 1992 (Ilatsia *et al.,* 2007).

In Kenya the breed is favoured by the Maasai pastoralists due to its high milk production and growth as well as good reproductive ability compared to the local zebu (Ilatsia *et al.,* 2007; Ilatsia *et al.,* 2011). Therefore the breed is a very important dual purpose cattle breed for pastoral and mixed farming communities in the Eastern African region (Muhuyi, 1997). The breed fits well within the harsh rangelands of East Africa because the agro-climatic conditions of these rangelands are similar to the breed's original habitat in the Punjab region of India and Pakistan (Muhuyi, 1997).

2.2   Sahiwal cattle production systems in Kenya

The Sahiwal cattle in Kenya are mainly raised by Maasai pastoralists in the Arid and semi-arid areas of Kenya. However, pure Sahiwal cattle are found in government and private ranches (Roessler *et al.,* 2010). The government and private ranches form the nucleus of the Sahiwal cattle breeding programme in Kenya. The breeding strategies adopted are pure breeding by the nucleus herds and crossbreeding among the pastoralists. The nucleus herds therefore produce bulls for pure breeding and crossbreeding in the pastoral herds. Breeding takes place under a closed nucleus, where movement of genes is unidirectional, from the nucleus to the pastoral herds, which form the commercial population. Cattle in the pastoral herds as well as those in government and private herds are raised under low input production

systems where the purpose is for tangible and intangible benefits (Roessler *et al.,* 2010). The main aim of Sahiwal farmers in the different production systems is to increase milk yield, body size and mature weight. Good fertility and adaptation to local production conditions are also considered (Ilatsia *et al.,* 2011).

2.3 Breeding objective for the Sahiwal cattle in Kenya

Before any genetic improvement programme is implemented, the breeding objective must be defined (Aby *et al.,* 2012). The breeding objective comprises traits which the producer attempts to improve genetically because they influence returns and costs. Development of breeding objectives involves specification of the breeding, production and marketing systems, identification of sources of income and expense, identification of biological traits influencing revenue and costs, derivation of economic and biological values, estimation of genetic and phenotypic parameters and prediction of genetic gain. For the Kenyan Sahiwal, these steps have been covered in recent studies (Roessler *et al.,* 2010; Ilatsia *et al.,* 2011).

The breeding objective for the Sahiwal cattle, which targets traditional markets, includes sale weight (kg), lactation milk yield, feed intake, age at first calving, cow weight, calving interval, pre-weaning survival, post-weaning survival and productive lifetime. The breeding objective as presently defined (Ilatsia *et al.,* 2011; Ilatsia *et al.,* 2012) includes a measure oflongevity, but it is important to note that genetic parameters of longevity for the population are lacking. Use of parameters from other livestock populations, albeit being raised under the same production system or climatic conditions as the Sahiwal cattle, as in any other improvement programme implies that the trait may be influenced by other traits indirectly, resulting either in a favourable or unfavourable genetic change (Kern *et al.,* 2014a,b).Therefore it is important to estimate genetic parameters for the Sahiwal cattle in Kenya and its relationship with other breeding goal traits.

2.4 Definition of longevity

Longevity traces time from a defined starting point up to the occurrence of an event (Ducrocq *et al.,* 1988; Beswick *et al.,* 2004; Flynn, 2012). In the context of this thesis, the defined starting point can be time of birth or first calving up to the last test day record or last day in milk, or the time when an animal exits a herd. Longevity can be true or functional longevity.

Functional longevity is the ability of a cow to delay culling on whatever basis, other than milk production. The implication in this case is that the animal has above average health, fitness and fertility (Bünger and Swalve, 1999; Zavadilová and Štípková, 2012). Measures of functional longevity include number of lactations, age from first calving to last day in milk, length of productive life and lifetime production (Ducrocq *et al.,* 1988). The uncensored definitions of longevity are based on age at exit, either through culling or death.

Censored definitions of longevity are related to survival to a pre-determined age within or across lactations (Jamrozik *et al.,* 2008; Forabosco *et al.,* 2009). Defined this way, longevity can be scored as a binary trait, where animals are scored as to whether they survived to a given age or not (Holtsmark *et al.,* 2009; Du Toit, 2011). The trait can be analysed using linear regression models (Veerkamp *et al.,* 2001; VanPelt and Veerkamp, 2014) or threshold models (Holtsmark *et al.,* 2009). The period can be limited to within lactation (Holtsmark *et al.,* 2009) or across all lactations (Van Pelt *et al.,* 2015). This definition is limited by the fact that only animals that survive to a given age are include in the genetic analysis, while those which are still surviving are left out. Further, animals that exited before the specified period are excluded since they are considered missing (Veerkamp *et al.,* 2001). Longevity can also be regarded as stayability, which is the probability that a cow will survive to a certain age, if it is given the opportunity to attain that age (Maiwashe *et al.,* 2009). Another definition is the time in days between calvings, or from one calving to death or culling (Sewalem *et al.,* 2005a). Other definitions of longevity include number of days from calving to culling, death, censoring or second calving (herdlife in the first lactation) and number of days from calving to culling, death, censoring or sixth lactation (herdlife in the first five lactations). Survival scores for the first five lactations or survival to 365 days (0 if a cow was culled before 365 days or 1 if it reached at least 365 days) (Holtsmark *et al.,* 2009) have also been used to define longevity.

2.5 Importance of longevity in cattle breeding

Removal of a cow from the herd occurs primarily due to reproductive failure, production of poor quality calves or low milk production. The importance of longevity is clearly understood when viewed against the value of removal and the cost of replacement. In beef cattle, a cow's peak performance and profitability is about 9 years of age. From a production perspective, the

optimal age of exit from a herd has also been found to be about 9 years of age (Garcia *et al.,* 2015). From an economics perspective, selecting for increased longevity has a positive impact on profitability of cattle enterprises (Garcia *et al.,* 2015) through lowered costs of replacement. Despite its importance in cattle breeding, longevity is not considered in routine genetic evaluation of Sahiwal cattle and its genetic parameters have not been estimated (Ilatsia *et al.,* 2011; Ilatsia *et al.,* 2012). Recently, higher production costs have led to an increase in prices of calves, cattle, and beef prices are pushing the costs of purchasing replacement cows and heifers up. To counter this trend cows can be selected for longer productive life. Selecting for longer productive life leads to positive economic impact (Garcia *et al.,* 2015).

2.6   Economic value of longevity

As a trait, longevity has many definitions, all which aim at describing the importance of an animal's lifespan in relation to its contribution to profitability of a herd. Regardless of the definition adopted, it is generally agreed that longevity is a trait of major economic importance in cattle and greatly influences herd profitability (Essl, 1998; Schneider *et al.,* 1999; Sewalem *et al.,* 2005b). Longer longevity is an indication of lower incidences of involuntary culling and implies an increased proportion of higher producing mature cows in the herd leading to improved herd production. A positive consequence of this herd structure is that replacement requirements are lowered, meaning more surplus heifers are available for sale. Cow maintenance costs are also spread over a large number of offsprings. A Higher selection intensity among cows is possible since involuntary culling and replacement requirements are reduced.

Numerous cattle breeding programmes have incorporated longevity in their breeding objectives due to its high economic importance (Wesseldijk, 2004; Miglior *et al.,* 2005; Banga *et al.,* 2013). As breeding programmes focused on increasing yield, there has been an associated decline in fitness traits such as longevity, udder health and fertility (Dube *et al.,* 2008; 2009). This has necessitated inclusion of such traits in the breeding objectives for many cattle breeding programmes. Increase in longevity has been found to result in increased profits in various cattle breeding programmes (Wolfová *et al.,* 2007; Banga *et al.,* 2013), although it was found to be breed dependent (Banga *et al.,* 2013). By definition, the economic value of a trait is the expected increase in profit due a unit improvement in the

genetic merit of a trait when all other traits in the breeding objective are held constant (Hazel, 1943). It can also be defined as the change in farm profit per cow per year due to a unit change in genetic merit of the trait of interest (Vargas *et al.,* 2002).

2.7   Direct selection for longevity

In cattle herds longer productive herds means that few replacement heifers are required (Setati *et al.,* 2004). Replacement of cows by heifers in a herd is necessitated by involuntary factors of production, such as problems related to udder ligaments, angulation, diseases, infertility and low speed of milking. On the other hand, cows can be disposed through voluntary culling due to low production of milk (Sewalem *et al.,* 2008). Involuntary disposal is an indicator of the status of animal welfare and is therefore done to reduce suffering. However, a high rate of involuntary culling in most cases is indicative of underlying problems associated with herd management. The price of the culled cow is usually lower than that of the replacement heifer, meaning that involuntary culling is a costly strategy (Kadarmideen *et al.,* 2005). Some of the criteria used in cow herds to select animals for disposal include poor fertility, serious health problems, high somatic cell count, physical defects and low production (Quieroz and Mcallister, 2002).

Heritability estimates for longevity regardless of how the trait is defined or analysed are low (Van Pelt *et al.,* 2015; Kern *et al.,* 2014a,b; Ahlman *et al.,* 2011). However, due to its great relative economic importance in cattle (Banga *et al.,* 2013), longevity is being included in the breeding objective of cattle breeding programmes. Even though it has a low heritability estimate, direct selection for longevity may yield significant gains (Kern *et al.,* 2014b), especially when generation interval is considered.

2.8   Indirect selection for longevity based on linear type traits

Due to the realization of the importance of longevity, most breeding programmes are changing to include longevity in their breeding goals (Forabosco *et al.,* 2009; Banga *et al.,* 2013). However, direct selection for longevity is limited by the long time needed to obtain the required information, sometimes after the death of the cow (Lagrotta *et al.,* 2010) and low heritability, ranging from 0.03 to 0.13 (Van Pelt *et al.,* 2014). Although milk production is given a lot of emphasis in the breeding goal of the Sahiwal cattle breeding programme as presently defined (Iltasia *et al.,* 2011), knowledge of its association with other traits is

important as it can is lead to deterioration of other traits of economic importance (Albarran-Portillo *et al.,* 2013).

Linear type traits are being used to select for conformation, reproduction and longevity. This is because the genetic correlations between some type traits and longevity for cattle populations have been reported to be favourable (Kern *et al.,* 2014a). Inclusion of type traits leads to the improvement of a cow's conformation, functional and reproductive structure for the cow to meet the challenges of increasing production. Apart from the favourable genetic correlation with longevity, type traits are moderately heritable (Kern *et al.,* 2014b) and are recorded early in an animal's life (Cruishank *et al.,* 2002; Kadarmideen *et al.,* 2005).

The benefits of indirect selection for longevity using type traits include reduction of involuntary culling leading to increased profitability because culling is based on milk production. Type traits with great influence on longevity include those related to udder, feet and legs (Kern *et al.,* 2014b; Sewalem *et al.,* 2008). Selection for some of these traits has been shown to improve longevity and even 305 milk yield (Kern *et al.,* 2014a). Generally, indirect selection for longevity based on linear type traits will not yield significant changes in these traits due to low genetic correlations. Nevertheless, due to the low heritability for longevity, indirect gain due to selection on type traits which have high heritability estimates can yield up to 20% more gains in longevity compared to direct selection (Kern *et al.,* 2014c). Therefore, indirect selection for longevity based on type traits may not be very efficient, but is justifiable since these traits are measured early in life.

In the Kenyan Sahiwal cattle population, type traits are not routinely recorded, but the breeding objective includes traits such as production and fertility traits (Ilatsia *et al.,* 2011). However, the genetic correlations in the current breeding objective traits and longevity have not been estimated. It is therefore not known whether correlated response in longevity due to selection on the current selection criteria would be favourable or not. Reproductive traits, apart from being important determinants of herd productivity, have been shown to contribute to longevity in cattle herds (Sewalem *et al.,* 2008). Poor reproductive performance leads to prolonged calving intervals (Muasya *et al.,* 2015a) and sometimes also increased involuntary culling. Consequently, a cow produces less milk and fewer calves per year and its lifetime. Increased involuntary culling because of sub-optimal fertility can also lead to high replacement costs (Kadarmideen *et al.,* 2005) thereby lowering net returns from cattle

enterprises. Therefore breeding objectives of many selection programmes across the world are being changed to include functional traits such as health and fertility (Sewalem *et al.,* 2010; Banga *et al.,* 2013).

Numerous studies have reported the genetic relationship between fertility traits and milk yield (e.g. Albarran-Portillo and Pollot, 2013) with only a few reporting on the association between fertility and longevity (Perez-Cabal *et al.,* 2006; Sewalem *et al.,* 2006; Sewalem *et al.,* 2008). Sewalem *et al.* (2008) found that reproductive traits were significantly associated with functional longevity. Cows that required more services per conception, had more days open and days from first service to conception were more likely to be involuntarily culled. A selection programme focusing on primarily increasing milk yield leads to deterioration in fertility (Sewalem *et al.,* 2010; Albarrán-Portillo and Pollott, 2013). This is due to increase in peak yield (Frigens *et al.,* 2007) which is associated with a negative energy balance at peak yield. It is therefore expected that in such a breeding programme, increasing milk yield will lead to increased involuntary culling due to poor fertility, thus compromising longevity and herd productivity.

2.9   Modelling of longevity

The global trend in cattle breeding is now to include all economically important traits in the breeding objective. Functional traits such as longevity, disease, fertility and type traits are now featuring prominently in the breeding objective of many breeding programmes (Zvandilova and Stickova, 2009; Banga *et al.,* 2014; Interbull, 2014). This is because the economic value of longevity is reported to be upto half of that of production traits (Jairath and Dekkers, 1994). In the quest to include longevity in the breeding objective, the first step has been to come up with a definition of longevity. To date, longevity is variously defined as length of productive life, lifetime milk production, herdlife, total number of lactations and survival from birth or first calving to a certain age (Vacek *et al.,* 2006; Varona *et al.,* 2012). The second challenge has been the choice of an appropriate analysis procedure. Here the challenge is basically because factors affecting longevity change over time.

Characteristically, longevity is a threshold trait, and displays distinct categorical phenotypes. Threshold traits are influenced by an underlying continuous liability (Falconer and MacKay, 1996). For longevity data, most animals in a herd are found in early lactation, hence the data

is usually skewed to the left (Caraviello *et al.,* 2004). Factors that influence longevity differ over time depending on prevailing environmental conditions and are therefore time dependent (Zavadilová *et al.,* 2011; Flynn, 2012). Survival data can be censored or uncensored. Events like death or culling may be known to have occurred and therefore will be uncensored. On the other hand such events may not have been recorded because they are not known to have occurred. If animals are alive at the time of analysis, they will be included in the evaluation and are therefore regarded as censored (Beswick *et al.,* 2004). These complex characteristics or features of survival data require careful consideration and choice of the appropriate modelling strategies in order to discover all phenotypic, additive and environmental variance (Weigel *et al.,* 2003). Approaches used in the analysis of longevity include linear models (Du Toit, 2011; Kern *et al.,* 2014). This method has been used for longevity measures defined quantitatively such as lifetime milk yield, age from birth or calving to last day in milk and total days in lactation. Other models include random regression (Van Pelt and Veerkamp, 2014), threshold, proportional hazard and random regression models (Van Pelt *et al.,* 2015).

2.9.1 Linear models

This approach accounts for censored data or records of cows which are still alive at the time of analysis. Survival of an animal to a predefined age or time period is used. The time period or age t, is pre-determined on a time scale and the record of each animal is assigned a 1 or 0, for successful survival to that age or not, respectively. The model is as follows:

$$y_{ij}(t) = \mu + s_i + e_{ij}$$

where $y_{ij}(t)$ =0 if the jth progeny of the ith sire did not survive to time *t* and 1 if it was alive at that time. μ is the overall popualtion mean, s_i is the breeding value of the ith sire on the binary scale and e_{ij} are random residuals. This approach to modelling longevity has been applied to Czech Fleckvieh (Zavadilová *et al.,* 2009b), South African Jerseys (Du Toit, 2012) among other cattle populations (Samore *et al.,* 2010; Zavadilová and Štípková, 2012). This approach is simple and can accommodate univariate as well as multivariate animal, sire or maternal grandsire models. The drawback of this model is that it makes unrealistic assumption that data are continuous and are normally distributed (Yazdi *et al.,* 2002). Animals that at different ages before the pre-determined time point are treated the same way, leading to erroneous results (Ducrocq *et al.,* 1988). Factors that influence longevity over the

time period are not considered, since survival times are derived from a product (Vukasinovic, 1999).

Linear models are more appropriate in analysing continuous traits such as milk yield rather than binary traits. This is the caution that was taken by Kern *et al.* (2014b). in this study measure of longevity which were continuous e.g. lifetime milk yield, age from birth or first calving to last day in milk, total days in milk over all lactations were analysed using linear models, while measures of longevity related to survival were analysed using threshold models. This was necessary because use of linear model BLUP was inappropriate because with categorical, data breeding values and residuals would not be independent of each other (Gianola, 1982).

2.9.2 Random regression models

Random regression models model additive genetic values as a function of an observed dependent variable through a set of random coefficients. In modelling survival data using random regressions, animal records are assigned binary units (0 or 1) if it survived a lactation or a month after calving. A linear model with random regressions for additive animal effect as random effects is then fitted for genetic evaluation and breeding values generated for any point in the trajectory (Jamrozik *et al.,* 2008; Van Pelt *et al.,* 2015). A univariate random regression model is described as follows:

$$y_{ijklmno:t} = (YS:Ht)_{ij} + (YSAP:t)_{ikl} + r(a, xm1)_n + r(pe, x, m2)_k + e_{ijklmno:t}$$

where $y_{ijklmno:t}$ is the nth observation of the kth animal at time t of the ith fixed effect and j^{th} group, YS is the ith year-season of first calving, H is the jth herd, A is the kth age at first calving class, P is the production level, $y_{ijklmno:t} = \sum_{i=0}^{m_1} a_{kl} x_{ijk:l}$ is notation for random regression, whwre a is the additive genetic effect for the kth animal, x are orthogonal polynomials of time t, after calving, *a* is the random regression coefficients for additive genetic effects for animal n, *pe* are the random regression coefficients for permanent environmental effects for animal n and $e_{ijklmno:t}$ are random residuals. Random regression models are more robust to effects of censoring data (Veerkamp *et al.,* 1999) and are closer to proportional hazard models and generalized linear models. They can also handle multiple traits (Jairath *et al.,* 1998).

2.9.3 Proportional hazard models

Proportional hazard (PH) models model survival as the probability that an animal will survive past a specified time t, and the hazard function, which is the instantaneous rate of failure (Ducrocq, 2005). The survival function and the hazard functions in PH modelling differentiates between a cow that dies exactly at time t, and one that was last alive at time t, and may have survived on. PH models make the assumption that the hazard rate or risk is a function of time-dependent baseline hazard and an exponential function of a series of explanatory variables i.e. covariates (Ducrocq, 1997). PH models may not result in the best fit to data and therefore may not accurately estimate the performance of future offsprings of an individual (Holtsmark *et al.,* 2009). They also make the assumption that survival is the same trait throughout the lifetime, although correlations between parities 1 to 3 have been reported to be less than unity. Another limitation is their inability to account for non-random mating among animals (Boettcher *et al.,* 1999) and cannot handle multiple traits (Holstmark *et al.,* 2009; Veerkamp *et al.,* 2001). Despite these limitations they are able to handle censored data and can accommodate non-normal data distribution well and incorporate time-dependent environmental effects (Ducrocq *et al.,* 1988). Common PH models include Weibull and Cox models, with the former being more popular.

2.9.4 Threshold models

In threshold modelling, survival is considered as a binary trait (0=dead at time t and 1=alive at time t). Threshold models include sequential threshold models, threshold repeatability models, and threshold cross-sectional models. Threshold models have been used to evaluate survival to weaning in pigs (Cechinnato *et al.,* 2010), survival in dairy cattle (Holtsmark *et al.,* 2009). Threshold models have been used to analyse measures of longevity related to survival such as survival from birth or first calving to predetermined age (Kern *et al.,* 2014a). The major limitation of threshold models is that heritability estimates are from an underlying continuous scale, and their effect on rate of genetic gain may be similar to that from linear models (Boettcher *et al.,* 1999). However, they are capable of handling multiple traits and can handle large datasets.

2.9.5 Model comparison

Linear, threshold and random regression models yield lower estimates of heritability, ranging from 0.01 to 0.18 (Kern *et al.,* 2014a,b; van Pelt and VeerKamp, 2014) than proportional hazard models (0.15 to 0.22) on the original scale. However, the former group of models is able to accommodate multiple traits and therefore can produce genetic correlations of

longevity with other indicator traits (Kern *et al.,* 2017). Holtsmark *et al.* (2009) found that threshold models yielded higher heritability estimates (0.04) compared to those obtained from linear repeatability and cross-sectional models (0.02). In terms of accuracy of evaluations, the models were compared based on the correlation between true and estimated breeding values for proportion of sire's daughters that survived to a specified age and sire ranking. The correlation for Weibull models remained constant over time, but increased over time for linear and random regression models, though they were lower than for the former models. The models also differed in terms of ranking of sires. For instance, linear models and Weibull models had similar sire rankings compared to proportional hazard models. Multi-trait models were also found to be superior in terms of predicting survival of daughters up to a certain age compared to Weibull models (Jamrozik *et al.,* 2008). In this study, Weibull models showed poor prediction of proportion of daughters of sires in early cow lifetime than multiple trait models.

In general, linear and threshold models have been found to be superior to Weibull models when sire breeding values are estimated when predicting survival to 365 days from first calving (Holtsmark *et al.,* 2009). Weibull models are better when predicting functional longevity while linear random regression and linear multiple trait models are the models of choice when predicting overall survival (Jamrozik *et al.,* 2008). Linear models are however favoured when studying the predictive ability of sire estimated breeding values of survival to a particular age, since this is better measured by average longevity instead of functional longevity. Threshold models are more appropriate for analyzing binary survival than linear models (Boettcher *et al.,* 1999), while linear multiple trait and random regression models resulted in inferior statistical correctness (inferior model fit) (Jamrozik *et al.,* 2008). Threshold sire models also result in higher heritability estimates than linear sire models

2.10 Heritability estimates for longevity

Longevity is the single most important functional trait in cattle breeding with a high economic value but has very low heritability. Van Pelt *et al.* (2015) reported heritability estimates for longevity defined variously based on the length of time interval for survival after first calving as ranging from 0.002 to 0.031. In another study, Kern *et al.* (2014b) reported estimates ranging from 0.05 to 0.07 for longevity defined as total milk production over all lactations, number of lactations initiated, total number of days in lactation over all lactations, time between birth and last milk recording in months; and time from first calving

to last milk recording in months. In another study, Kern *et al.* (2014b) reported heritability estimates of 0.06 to 0.09 using the linear model and 0.05 to 0.18 for traits using the threshold model for Brazilian Holstein cows. Other studies that have reported low to moderate estimates of heritability for longevity include Ahlman *et al.* (2011) and M'hamd *et al.* (2014). Thus heritability estimates for longevity regardless of how the trait is defined or analysed are low, implying that direct selection may not yield significant gains (Kern *et al.,* 2014b).

It is however important to note that estimates of heritability for longevity depend on the model used for analysis. For instance estimates from proportional hazard models can be expressed either on a log linear scale, original scale or as effective heritability (Yazdi *et al.,* 2002). Heritability estimates from linear, threshold or random regression models are usually lower than those from proportional hazard models (Ducrocq, 2002; Sewalem *et al.,* 2005a). Estimates ranging from 0.01 to 0.03 for length of productive life defined as a binary trait were reported for South African Jerseys from multivariate linear sire and animal models (Du Toit, 2011). Slightly higher estimates (0.06) using a linear animal model were reported for South African Holsteins (Setati *et al.,* 2004). Higher estimates from linear animal models ranging from 0.05 (Zavadilová *et al.,* 2009) to 0.1 (Tsurata *et al.,* 2005) have been reported for Czech Fleckvieh and American Holsteins, respectively.

Estimates of heritability based on random regression models are reported for monthly survival. This way if an animal survived to month n+1, it is considered alive and assigned a score of 100. A cow culled in month n is assigned a score of 0 (Van Pelt and Veerkamp, 2014). Monthly survival heritability estimates have been reported to range from 0.002 to 0.011 (Van Pelt and Veerkamp, 2014). Van Pelt *et al.* (2015) reported estimates ranging from 0.002 to 0.031. Cumulative heritability estimates over the entire life span ranged from 0.115 to 0.149 (Van Pelt and Veerkamp, 2014; Van Pelt e*t al.,* 2015). Higher ranges for monthly estimates of 0.02 to 0.181 (Forabosco *et al.,* 2009) and 0.01 to 0.07 (Veerkamp *et al.,* 2001) for British dairy cattle have been reported. Jamrozik *et al.* (2008) reported higher estimates, ranging from 0.12 to 0.36 for Canadian Jersey cattle.

Heritability estimates for longevity estimated using threshold models have been reported for various cattle populations. Holtsmark *et al.* (2009) reported an estimate of 0.04 for Norwegian Red Holsteins while Kern *et al.* (2014) found a value of 0.15 for Brazilian Holsteins. Higher estimates for beef cattle ranging from 0.08 (Van Westhuizen *et al.,* 2001)

to 0.30 (Maiwashe *et al.,* 2009) have been reported. The differences between estimates for dairy and beef cattle could partly be due to differences in definition of longevity and breeding objective. Gonzalez-Recio and Alenda (2007) reported an estimate of 0.11 using a sequential threshold model. In general threshold models yield higher heritability estimates than linear models.

Heritabilities obtained from proportional hazard models estimated on the original scale are usually higher than those on log linear scale, and are similar to those from linear models (Ducrocq and Solkner, 1998). Estimates from log linear scale range from 0.05 to 0.10 (Caraviello *et al.,* 2004b) and 0.15 to 0.20 on the original scale (Caraviello *et al.,* 2004a). using a Weibull Porportional hazard model, Mészáros *et al.* (2008) reported heritability estimate of 0.05 on the log scale for Pinzgau cattle in Croatia, similar to 0.04 reported by Van der Linde *et al.* (2006) and Chirinos *et al.* (2007). Higher estimates of 0.16 to 0.22 (Ducrocq), 0.12 (Egger-Danner et al., 2005) and 0.21 to 0.22 (Bünger and Swalve, 1999) on the original scale have also been reported. Other heritability estimates for various definitions of longevity are summarized in Table 2.1. The wide variation in estimates of heritability could be attributed to differences in magnitudes of genetic variation for longevity, differences in accuracy of sire identification, record keeping and precision of data analysis and model used (Caraviello *et al.,* 2004b).

2.11 Genetic correlations between longevity and performance traits

Estimation of genetic parameters for traits expressed early in an animal's life and their correlation with longevity can help to identify a selection criterion, which enables the inclusion of longevity in the breeding goal of the Kenyan Sahiwal population. This will lead to development of a more comprehensive breeding objective ensuring sustainable genetic improvement of the breed. Genetics correlations between longevity and performance trait depend on the type of trait population being studied and the way longevity is defined. For instance, Kern *et al.* (2014b) reported that genetic correlations between various definitions of longevity and linear type traits ranged from -0.39 to 0.31. In this study, longevity was defined either as total milk yield over all lactations, number of lactations initiated, time between birth and last milking record in months, time between first calving and last milking record in months or total number of days in lactation over all lactations. Longevity defined as total number of days in lactation over all lactations had the strongest genetic correlation with type

traits such as weight (-0.38), stature (-0.31), topline (-0.25), chest width (-0.27), udder width (-0.30) among others. Longevity defined this way was also positively correlated to rump angle, bone quality, udder height and udder depth (Kern *et al.,* 2014b). Other studies reported genetic correlations between rump width and number of days in lactation, number of lactations initiated and time between birth and last milking record of -0.27, -0.15 and -0.29, respectively, in Jersey cattle (Zavadilová and Štípková, 2012).

Genetic correlations between fore udder and longevity traits have been reported to be low, ranging from 0.06 to -0.08 (Zavadilová *et al.,* 2009a; Zavadilová and Štípková, 2012; Kern *et al.,* 2014) suggesting that selection based on fore udder attachment, fore teat placement and fore teat length has little influence on longevity. However, longevity was moderately correlated with rear udder height (0.16 and 0.20), indicating that selection based on these traits may favor the permanence of cows in the herd. Udder depth had the highest positive genetic correlations with measures of longevity, ranging from 0.17 to 0.31 (Kern *et al.,* 2014b).

Table 2.1 Heritability estimates for various definitions of longevity

Breed	N	Trait	Heritability	Author(s)
German Holsteins	11 106	FL	0.03-0.05	Wiebelitz *et al.*(2014)
Czech Holsteins	57 803	NL	0.05	Zavadilova and Stipkova (2012)
Czech Holsteins	57 803	NLF	0.04	Zavadilova and Stipkova (2012)
Czech Holsteins	57 803	LPL&FLPL	0.03	Zavadilova and Stipkova (2012)
South African Jersey	181 269	FHL	0.02-0.03	Du Toit (2011)
South African Jersey	181 269	FHL	0.01-0.03	Du Toit (2011)
Norwegian Red	808 750	SS	0.02-0.03	Holtsmark *et al.* (2009)
Czech Fleckvieh	58 493	FL	0.05	Zavadilova *et al.* (2009)
South African Holsteins	34 201	NL	0.06	Setati *et al.* (2004)
Japanese Holsteins	117 404	HL	0.12-0.12	Sasaki *et al.* (2012)
Tunisian Holsteins	36 888	FL	0.19	M'hamdi *et al.* (2010)
Japanese Holsteins	158 719	FLPL	0.05-0.10	Terawaki and Ducrocq (2009)
Norwegian Red	808 750	PL	0.04	Holtsmark *et al.* (2009)
Slovak Pinzgau	21 985	FLPL	0.05	Mészáros *et al.* (2008)
Spanish Holstein-Friesian	21 058	FL	0.05-0.07	Chirinos *et al.* (2007)
French Holsteins	629 716	FL	0.22	Ducrocq (1997)
Brazilian Holsteins	-	SGA	0.09-0.15	Kern *et al.* (2014)
Norwegian Red	808 750	SS	0.04	Holtsmark *et al.* (2009)
Norwegian Red	808 750	SS	0.04	Holtsmark *et al.* (2009)
South African Beef Breeds	-	FL	0.08	Van der Westhuizen *et al.* (2001)
Canadian Holsteins	700 000	FL	0.07	Boettcher *et al.* (1999)
Spanish Holsteins	96 642	SNL	0.11	Gonzalez-Recio and Alenda (2007)
South African Angus	28 671	Stayability	0.24-0.30	Maiwashe *et al.*(2009)

Dutch Dairy Cattle	950 616	FL	0.002-0.01	VanPelt and Veerkamp (2014)
Canadian Jersey	1 164	Stayability	0.12-0.36	Jamrozik *et al.*(2008)
British Holsteins	24 741	FL	0.01-0.07	Veerkamp *et al.*(2001)

NL :number of lactations initiated; FLPL: functional length of productive life; FHL: functional herdlife; FL: functional longevity; LPL: length of productive life; SNL: survival to next lactation; SS :survival scores; SGA: Survival to given age.

The choice of which trait to use a selection criterion for longevity depends on its heritability, cost, ease of measurement and time required to obtain its information. Based on the study by Kern *et al.* (2014b), selection for udder depth in the first lactation, since this trait has higher heritability (0.23 to 0.26) than longevity measures (0.05 to 0.07), has a lower cost as it is collected early in life and presents moderate correlations with longevity (0.17 to 0.31), and, therefore, can be used as a proxy for indirect selection for longevity.

2.12   Inbreeding depression for longevity and other survival related traits

The current quest of cattle improvement programmes world over is to improve longevity alongside other traits of economic importance. Despite its economic importance to cattle farming, studies of inbreeding depression on longevity are very few. However, longevity and other correlated traits are negatively affected by inbreeding in livestock populations. For instance, longevity and reproductive performance decreases while, rate of disposal or loss of replacement heifers before first calving, age at puberty increases due to inbreeding through reduced growth (Du Toit *et al.*, 2012). For every increase of 1% in inbreeding, productive life was reported to decrease by about 13 days (CDN, 2008). Cows with high inbreeding level also have a higher risk of being culled (Rokouei *et al.*, 2010).

In cattle dairy cattle the detrimental effects of inbreeding on production traits are well documented. A 1% increase in inbreeding coefficient level has been found to decrease milk production by 37kg (CDN, 2008). A similar increase in inbreeding resulted in a 15.42kg milk yield in South African Jersey cattle (Mostert, 2011). Milk component traits, butter fat and protein yield were also negatively affected. Though inbreeding depression for production traits in dairy cattle is well documented, not many studies have reported on the effect of inbreeding on longevity of cows (Caraviello *et al.*, 2003; Sewalem *et al.*, 2006). In Canadian cows longevity was reduced by 65 days due to a change in inbreeding of 5% (CDN, 2008). Further, cows with high levels of inbreeding were reported to face a higher risk of being culled (Rokouei *et al.*, 2010). There is need to investigate inbreeding depression in longevity,

production and fertility traits in the Kenyan Sahiwal population based on individual level and rate of inbreeding.

Effects of inbreeding on non-production traits include decreased reproductive efficiency and decreased stayability. The negative effects on traits related to fitness have been attributed to reduced heterozygosity as inbreeding accumulates (Falconer and Mackay, 1996). Inbreeding level and rate of inbreeding in the Sahiwal cattle population in Kenya have been found to be on an upward trend and are above 1% (Mwangi *et al.,* 2016). Inbreeding depression for longevity and other correlated traits should be assessed for the Sahiwal cattle population in Kenya.

CHAPTER THREE

GENETIC PARAMETERS FOR MEASURES OF LONGEVITY IN KENYAN SAHIWAL CATTLE

3.1   Abstract

Performance data of Sahiwal cows born between 1972 and 2004 and with milk production records between 1976 and 2008 from the National Sahiwal Stud, Kenya, were anlysed to estimate genetic parameters for longevity. Measures of longevity related to productive life were time between birth and last milking record in months (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), total number of days in lactation over all lactations (Long_4) and total milk yield over all lactations (kg) (Long5). Measures of longevity related to survival were defined as survival from birth to 44 months (Long6_44), 56 months (Long6_56), 80 months (Long6_80), 92 months (Long6_92), 104 months (Long6_104), and 128 months (Long6_128). An alternative measure was survival from first calving as survival from for 12 months (Long7_12), 36 (Long7_36), 60 (Long7_60), 84 (long7_84) and 96 months (Long7_96) from first calving. Longevity measures related to productive life were analysed using linear models while those related to survival were analysed via threshold models. Heritability estimates for measures of longevity related to productive life were low, and ranged from 0.038±0.032 for Long3 to 0.097± 0.04 for Long5. Estimates of heritability for longevity measures related to survival were higher and ranged from 0.084±0.053 to 0.119±0.035. However, survival from first calving to predefined ages had higher heritability estimated (0.090 to 0.119) compared to survival from birth (0.084 to 0.104). Estimates of heritability for longevity measures estimated using threshold models (survival measures) were higher than those estimated using linear models (measures related to productive life). Among measures of survival heritability estimates were highest in the later periods and were higher for survival from first calving than survival from birth. Survival from first calving to 96 months had highest additive genetic variance and heritability estimate, and therefore was the most efficient in estimating genetic variability and should therefore be used for genetic evaluation of longevity in Sahiwal cattle in Kenya. This study has also provided genetic and phenotypic parameters to enable inclusion of longevity in the breeding objective for the Sahiwal cattle improvement programme

Keywords: *Linear models, Kenya, Productive life, Sahiwal, Survival, Threshold models*

3.2   Introduction

Although milk production is considered as the single most important trait in dairy farming, cattle breeding programmes are changing their breeding objectives to include longevity and other traits (type and functional) (Banga *et al.*, 2013; 2014), so that cows can meet the challenges of high milk production. Longevity or the age at which a cow leaves the breeding herd is a trait of great economic importance in dairy and beef cattle breeding (Banga *et al.*, 2013). Productive longevity can also be described as the number of calvings per female (Varona *et al.*, 2012).

Direct selection for longevity results in improved health and fitness (Garcia *et al.*, 2015) and even milk production of cows (Kern *et al.*, 2014); therefore breeding for longevity is considered to have ethical and economic benefits since it results in favourable response in profitability of beef and dairy cattle enterprises (Garcia *et al.*, 2015). In beef and dairy cattle, longevity plays a considerable role in the farm economy by increasing the profit realised per cow and enables greater response to selection because fewer animals exit the herd due to involuntary culling (Logrotta *et al.*, 2010; Garcia *et al.*, 2015), a situation that provides greater selection intensity among females, and surplus heifers for sale (Banga *et al.*, 2013), contributing to the profitability is dairy and beef enterprises.

Longevity can be described variously as length of productive life, lifetime milk production, herdlife, total number of lactations and survival from birth or first calving to a certain age (Vacek *et al.*, 2006; Varona *et al.*, 2012). The inclusion of longevity in the breeding objective is hampered because the trait is lowly heritable (Caetano *et al.*, 2012; Kern *et al.*, 2014; Van Pelt *et al.*, 2015) and the delay in availability of phenotypic information (Lagrota *et al.*, 2010), which may lead to increase in generation interval (de Mello *et al.*, 2014). This is so when parameters for survival to a certain age are estimated via a linear model (Cruickshank *et al.*, 2002, Tsurata *et al.*, 2005; Daliri *et al.*, 2008). Higher estimates of heritability for survival have been reported when using threshold models (Ahlman *et al.*, 2011; Kern *et al.*, 2014). Higher heritability estimates can lead to higher rates of genetic gains for longevity in selection programmes. The objective of this study was to estimate variance components, genetic and phenotypic parameters for longevity for the Sahiwal breed in Kenya using linear and threshold models.

3.3 Materials and Methods

Performance data of Sahiwal cows born between 1972 and 2004 obtained from the National Sahiwal Stud at Kenya Agriculture and Livestock Research Organization (KALRO), Naivasha, such that the cows had production records 1976 to 2008. Production and reproduction data i.e. date of birth date of first calving, date of last milking, milk yield by parity for each cow were collected. Longevity was defined as related to productive life or survival.

Table 3.1: Data structure use for analysis of measures of longevity for the Sahiwal cattle in Kenya

Measure of longevity	No. of animals with records	Number of sires
Time between birth and last milking record in months	2524	303
Time between first calving and last milking record in	1991	302
Number of lactations initiated	2707	317
Total number of days in lactation over all lactations	2707	317
Total milk yield over all lactations (kg)	1990	303
Survival from birth to 44 months	1887	209
Survival from birth to 56 months	1806	201
Survival from birth to 80 months	1623	178
Survival from birth to 92 months	1433	163
Survival from birth to 104 months	1292	145
Survival from birth to 128 months	1012	138
Survival from first calving to 12 months	1507	169
Survival from first calving to 36 months	1411	153
Survival from first calving to 60 months	1121	122
Survival from first calving to 84	915	106
Survival from first calving to 96 months	862	96

Measures of longevity related to productive life were: time between birth and last milking record in months (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5).

Measures of longevity related to survival were defined as survival from birth to 44 months (Long6_44), 56 months (Long6_56), 80 months (Long6_80), 92 months (Long6_92), 104 months (Long6_104), and 128 months (Long6_128). An alternative measure was survival from first calving as survival from for 12 months (Long7_12), 36 (Long7_36), 60 (Long7_60), 84 (long7_84) and 96 months (Long7_96) from first calving. The data structure in terms of number of cows, sires and dams of cows and contemporary groups for measures of longevity are shown in Table 3.1. Measures of longevity related to survival were recorded as 1 for a cow that remained in the herd and 0 for those that were not in the herd at a particular age. Cows that were still alive at the time of analysis were excluded.

3.4   Data analysis

Variance components, genetic and phenotypic parameters for longevity were estimated using a linear model using the expectation maximization method in WOMBAT (Meyer 2007) using a convergence criterion of 10^{-9}. The analysis was restarted at each convergence and the values obtained in the previous convergence used as initial values for the new analysis until there occurred no change at the 4th decimal value of -2Log Likelihood in successive runs. The statistical model was:

$$y = X\beta + Za + e$$

where y, β, a and e are vectors of observation for longevity measures, fixed effects (contemporary group, first lactation milk yield class and age class at first calving), random additive genetic effects and random residual effects, respectively. X and Z are incidence matrices linking fixed and random additive genetic effects to observations, respectively.

For survival traits an additional threshold effect was fitted. Assumptions for random additive genetic effects and threshold model were: $a/G \approx N[0,G]$, where $G = A\sigma_a^2$; $e/R \approx N[0,R]$, where $R = I\sigma_e^2$; $G/u_a S_a \approx IW(u_a S_a, u_a)$; $R/u_e S_e \approx IW(u_e S_e, u_e)$ where G, R, A, I are matrices of additive genetic, residual, kinship coefficient and identity variances, respectively; σ_a^2 and are σ_e^2 additive genetic and residual variances, respectively; IW is the inverted Wishart distribution; u_a, S_a, and u_e and S_e are priori values and degrees of freedom for direct additive genetic and residual variances, respectively.

Longevity measured as survival from birth or first calving was analysed as threshold traits assumed to have an underlying continuous distribution. The threshold model relates survival to a given age in a categorical scale with a normal underlying continuous scale, U. The underlying continuous scale, U was assumed to have a normal distribution: $U|\theta \approx N\left(W\theta, I\sigma_e^2\right)$, where $\theta=(b',a')$ is a vector of location of parameters with b=fixed effects (as defined from a frequentist point of view) and a=random additive effects; W and I are known incidence and identity matrix, respectively, and σ_e^2=residual variance. The prior distributions for residual and direct additive genetic effects were assumed to follow multivariate normal distributions as follows: $p\left(a/\sigma_a^2\right) \approx N\left(0, A\sigma_a^2\right)$ and $p\left(e/\sigma_e^2\right) \approx N\left(0, I\sigma_e^2\right)$, respectively, where A is the numerator relation matrix; σ_a^2, σ_a^2 and I are additive genetic variance, residual variance and identity matrix, respectively. The linkage between the categorical and continuous scales can be established unequivocally based on the contribution of probability of an observation belonging to the first category being proportional to:
$P\left(y_v = 0 | 0\right) = P\left(U_v \leq t | t, 0\right) = \phi\left(\left(t - w_v'\theta\right)\right)$, where y_v is the response variable to the Vth observation, assuming values of 0 or 1 for an observation in first or second category, respectively; t and U_v are the threshold value and value underlying variable, respectively; ϕ is the cumulative distribution function of a normal standard variable and w_v' is an incidence column vector linking θ to the Vth observation.

Variance components for survival measures were estimated via Bayesian inference using THRGIBBS1F90 (Misztal *et al.,* 2002). Outputs from this software were used to obtain a posteriori estimates using POSTGIBBSF90 (Misztal *et al.,* 2002). Convergence of all Bayesian analyses were verified using the R program using Geweke's (1992) and Heidelberger and Welch (1983) diagnostics, from the Bayesian Output Analysis Program – BOA (Smith 2005).

3.5   Results

Sahiwal cows produced 3425.5 ±3534.2 kg of milk throughout a productive life of 2.73 ± 1.44 lactations (Table 3.2). The number of lactations initiated (Long3) ranged from 1 to 11. The average days in milk during productive life were 1172.7±703.7 days and ranged from 960 to 6246 days. The period of time that cows remained in the herd from birth (Long1) or

from first calving (Long2) to last day in milk was 2231.1±887.8 days and 1172.7±703.7 days, respectively.

Table 3.2: Means, standard deviations, minimum and maximum for longevity measures related to productive life for Sahiwal cattle in Kenya

Measure	Mean	Standard deviation	Minimum	Maximum
Long1, days	2231.1	887.8	960.0	6246.0
Long2, days	1172.7	703.7	226.0	4720.0
Long3, count	2.7	1.44	1.0	11.0
Long4, days	738.0	428.4	10.0	3147.0
Long5, kg	3425.5	3534.2	10.0	11616.0

Longevity was defined as (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5)

Estimates of components of additive genetic and residual variances for measures of longevity related to productive life are shown in Table 3.3. Additive genetic variances were lower than residual variances for all measures of longevity related to productive life (Table 3.3). This implies that some factors causing differences between animals were not captured during the data recording process and were therefore not included in the model of analysis. The values of additive genetic variance ranged from 0.058 (Long3) to 366033 (Long5). Heritability estimates for measures of longevity related to productive life were low, with the highest being 0.097± 0.04 (Long5).

For measures of survival from birth, there was a decrease of 31.5% and 42.8% in the survival rate between birth to 36 months ((Long6_36) to 72 months (Long6_72) and from calving to 44 months and 96 months, respectively. Survival rates up to 12, 24 and 54 months from first

Table 3.3: Estimates of additive genetic variance (σ_a^2), residual (σ_e^2) and heritability estimates (h^2) for measures of productive life for the Sahiwal cattle in Kenya

Parameter	Long1	Long2	Long3	Long4	Long5
σ_a^2	25208.9	24740.5	0.06	8820.0	366033
σ_e^2	296090.1	318344.1	1.51	118783.2	3397910
h^2	0.078 ±0.038	0.072±0.027	0.038±0.032	0.069±0.034	0.097±0.037

Longevity was defined as (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5)

calving were similar to measures of survival from birth. The reduction in survival for both measures of survival to different ages indicates reduced ability of cows to persist in the herd due to voluntary or involuntary culling. Measures of estimated mean, median and mode of variance components and heritability were all similar, indicating that the posterior distributions of these parameters were more or less symmetric (Tables 3.4 and 3.5). Heritability estimates for measures of survival from birth ranged from 0.084 (Long6_44) to 0.104 (long6_128), and were lower than those estimated those estimated from first calving (Table 3.5).

Table 3.4: Posterior descriptive estimates for additive genetic variance (σ_a^2), residual (σ_e^2) and heritability estimates for measures of survival from birth for the Sahiwal cattle in Kenya

Parameter	Mean ±sd	Mode	Median	Min	Max	IC- 95%
Long6_44						
σ_a^2	0.092±0.071	0.113	0.082	0.010	0.162	0.010 to 0.153
σ_e^2	1.007±0.032	0.955	1.008	0.902	1.116	0.902 to 1.039
h^2	0.084±0.053	0.105	0.075	0.011	0.126	0.011 to 0.128
Long6_56						
σ_a^2	0.094±0.076	0.081	0.072	0.009	0.182	0.054 to 0.170
σ_e^2	1.017±0.036	0.979	1.006	0.905	1.110	0.892 to 1.053
h^2	0.085±0.058	0.076	0.067	0.010	0.141	0.057 to 0.139
Long6_80						
σ_a^2	0.112±0.061	0.092	0.093	0.010	0.183	0.010 to 0.182
σ_e^2	1.014±0.043	1.009	1.004	0.900	1.111	0.904 to 1.104
h^2	0.100±0.041	0.084	0.085	0.011	0.142	0.012 to 0.142
Long6_92						
σ_a^2	0.114±0.063	0.111	0.110	0.038	0.162	0.013 to 0.182
σ_e^2	1.004±0.049	1.005	1.003	0.897	1.111	0.913 to 1.125
h^2	0.102±0.042	0.099	0.099	0.040	0.127	0.014 to 0.139
Long6_104						
σ_a^2	0.127±0.075	0.192	0.117	0.010	0.219	0.010 to 0.269
σ_e^2	1.105±0.054	1.009	1.004	0.904	1.104	0.901 to 1.511
h^2	0.103±0.056	0.160	0.105	0.011	0.165	0.012 to 0.151
Long6_128						
σ_a^2	0.116±0.081	0.121	0.106	0.001	0.193	0.013 to 0.176
σ_e^2	1.007±0.064	0.996	1.001	0.907	1.107	0.920 to 1.117
h^2	0.104±0.057	0.108	0.094	0.001	0.148	0.014 to 0.136

Key: Longevity was defined as survival from birth to 44 months (Long6_44), 56 months (Long6_56), 80 months (Long6_80), 92 months (Long6_92), 104 months (Long6_104), and 128 months (Long6_128); sd=standard deviation, IC-95%=95% confidence interval for an estimate; Min and Max are the minimum and maximum values

Additive genetic variances for survival measures from first calving increased from twelve months after first calving (long7_12) to 96 months after first calving (long7_96). Heritability estimates ranged from 0.090 (long7_12) to 0.119 (long7_96). Heritability estimates for longevity measured as survival from birth or first calving to last day in milk (Table 3.3 and 3.4) were generally low compared to those related to productive life (Table 3.3).

Table 3.5: Posterior descriptive estimates for additive genetic variance (σ_a^2), residual (σ_e^2) and heritability estimates (h^2) for measures of survival from first calving for the Sahiwal cattle in Kenya

Parameter	Mean SD	Mode	Median	Min	Max	IC- 95%
Long7_12						
σ_a^2	0.099±0.006	0.071	0.076	0.007	0.110	0.016 to 0.098
σ_e^2	0.997±0.057	1.002	0.997	0.912	1.102	0.898 to 1.097
h^2	0.090±0.044	0.066	0.070	0.008	0.085	0.018 to 0.082
Long7_36						
σ_a^2	0.108±0.007	0.061	0.069	0.007	0.097	0.018 to 0.103
σ_e^2	0.999± .051	0.977	0.990	0.906	1.098	0.898 to 1.099
h^2	0.097±0.053	0.059	0.065	0.008	0.081	0.020 to 0.085
Long7_60						
σ_a^2	0.115±0.071	0.061	0.091	0.008	0.109	0.028 to 0.110
σ_e^2	1.005±0.054	1.012	1.009	0.895	1.097	0.900 to 1.110
h^2	0.103±0.043	0.057	0.083	0.008	0.090	0.030 to 0.090
Long7_84						
σ_a^2	0.117±0.007	0.071	0.081	0.007	0.110	0.024 to 0.163
σ_e^2	1.005±0.052	1.000	1.003	0.905	1.095	0.904 to 1.106
h^2	0.104±0.046	0.066	0.075	0.008	0.092	0.026 to 0.128
Long7_96						
σ_a^2	0.140±0.007	0.095	0.096	0.015	0.156	0.022 to 0.169
σ_e^2	1.008±0.056	0.994	1.004	0.908	1.113	0.901 to 1.115
h^2	0.119±0.035	0.087	0.088	0.016	0.123	0.023 to 0.132

Key: Longevity was defined as survival from first calving as survival from for 12 months (Long7_12), 36 (Long7_36), 60 (Long7_60), 84 (long7_84) and 96 months (Long7_96) from first calving; sd=standard deviation, IC-95%=95% confidence interval for an estimate; Min and Max are the minimum and maximum values

The number of cycles, burn-in and number of Markov chains chosen for the current analyses were sufficient to attain convergence of all posterior distributions of the parameters for

survival measures, presenting values greater than 0.05% of the Geweke's test. The highest heritability was obtained for total milk yield over all lactations (Long5).

3.6   Discussion

The average observed age from birth and calving to last day in milk of 74.4 months and 39.1 months, respectively reported in the current study were longer that 57.2 and 30.1 months, respectively, reported by Nilforooshan and Edriss (2004) for Iranian Holsteins. Kern *et al.* (2014) reported estimated of 60.1 and 33.5 months for Brazilian Holsteins, respectively. However, the estimates reported in the current study were similar to those reported for Simmental dairy cows of 72 and 47.5 months (Javanovac and Raguz 2011). The average number of lactations initiated of 2.7 was similar to estimates of 2.7 and 2.8 for Brazilian and United States Holsteins, respectively (Tsurata *et al.,* 2005; Kern *et al.,* 2014). A higher estimate of 3.4 was reported for Simmental dairy cows (Strapak *et al.,* 2011). The diversity of measures of survival measured as herdlife or productive life could be attributed to genetic and environmental differences between the populations. Lifetime milk production, total lactation length and age from calving to last day in milk cover an animal's productive life. These traits can therefore be used as an indicator of the efficiency of a production system since they include reproductive and productive information. The proportion of animals retained for long in a herd can be achieved through decreased incidences of involuntary or voluntary culling (Forabosco *et al.,* 2009). Increase in the proportion of longer lived animals in a herd is accompanied by increased milk production and lowered risk of involuntary culling, leading to increased herd profitability. This also led to the increase in additive genetic variance and heritability estimates for survival to 12 months to 96 months after first calving.

The number of cows that failed to survive to a pre-determined period as measured by survival measures amplifies the challenges associated with maintaining better producing cows. Such cows are likely to have feet, udder and or reproductive problems, leading to involuntary culling (Queiroz *et al.,* 2007). Measures of longevity related to herd life and survival as used in the current study are alternative measures. Each measure has its advantages and can be used for selection. Considerations in terms of merit include the period required to obtain the necessary information and whether the partial information provided by the survival measures is sufficient (Vollema *et al.,* 2000). Since information is obtained before an animal dies, survival measures to a specified age provides an opportunity to reduce generation interval and faster rate of genetic gain for longevity (Galeazzi *et al.,* 2010).

All measures of longevity used in the current study were associated with high estimates of residual variances and low estimates of additive genetic variance hence the low estimates of heritability. The heritability estimates found in the current study of 0.04 to 0.119 were within the range reported for different cattle populations across the world. Heritability estimates for cattle populations in temperate climatic conditions ranged from 0.02 to 0.10 (Vollema and Gröen 1996; Tsurata *et al.,* 2005) while in tropical conditions the range was 0.06 to 0.18 (Kern *et al.,* 2014; M'hamdi *et al.,* 2014). The low heritability estimates for measures of longevity could be partly attributed to exclusion of censored records. When records are not censored, survival analyses yields slightly lower heritability estimates for longevity (Forabosco *et al.,* 2006) possibly due to loss of genetic variation because of exclusion of censored records.

Survival from birth had lower heritability estimates (0.08 to 0.10) compared to survival from first calving (0.09 to 0.12). A similar trend was reported for Holstein cows in Brazil (Kern *et al.,* 2014). This could be attributed to the fact that the two measures deal with different periods in a cow's life and that survival from first calving is adjusted for first lactation milk yield. Heritability estimates for survival measures increased with increasing period for survival, indicating a decreasing influence of the environment as a cow matures. A similar trend has been reported in previous studies for different dairy cattle populations (Vollema and Groen, 1996; Ahlman *et al.,* 2011; Kern *et al.,* 2014).

The benefits arising from direct selection for longevity include improved health and fitness (Garcia *et al.,* 2015) as well as milk production of cows (Kern *et al.,* 2014). Longevity is influenced by culling decisions, whether voluntary or involuntary. An increase in longevity of cows due to decreased involuntary culling contributes to reduced replacement costs and greater selection intensity for milk yield. This results in greater genetic gains due to increased chances of voluntary culling (Logrotta *et al.,* 2010; Garcia *et al.,* 2015). Lower replacement rates also lead to surplus heifers for sale (Banga *et al.,* 2013), contributing to profitability of cattle enterprises. Breeding for longevity is therefore considered to have ethical and economic benefits since it results in favorable response in profitability of beef and dairy cattle enterprises (Garcia *et al.,* 2015). In the current study measures of longevity related to survival to predetermined ages had higher heritability estimates compared to measures related to productive life and should therefore be used as selection criteria for longevity.

Estimates of heritability for longevity measures (life time milk yield, total lactation length, number of lactations initiated, age from birth or first calving to last day in milk) obtained using linear models were lower compared to those estimated using threshold models (survival from birth or first calving to specified ages). A similar trend was reported by Kern *et al.* (2014) for Brazilian Holsteins. The estimates of heritability were also similar to those reported in the current study. The highest heritability estimates for survival measures were found for survival either from birth or first calving to the last age specified, similar to reports by Kern *et al.* (2014) for Brazilian Holsteins. These measures of longevity, analysed using threshold models, have been reported to have higher heritability estimated compared to linear models (Sousa *et al.,* 2000; Ahlman *et al.,* 2011; Kern *et al.,* 2014). Linear models yield lower estimates compared to survival models partly due to inclusion of censored records and time-dependent variables (Ducrocq *et al.,* 1988; Forabosco *et al.,* 2006) as the environmental conditions affecting cow survival changes over time. Estimates of heritability using threshold models in the current study were similar to those found using similar models in Brazilian and Swiss Holsteins (Alman *et al.,* 2011; Kern *et al.,* 2014).

The inclusion of longevity in the breeding objective is hampered because the trait is lowly heritable (Van Pelt *et al.,* 2015; Kern *et al.,* 2014) and the delay in availability of phenotypic information (Lagrota *et al.,* 2010), which may lead to increase in generation interval (de Mello *et al.,* 2014). However, as demonstrated in the current study and other studies, (Vacek et al 2006; Varona *et al.,* 2012; Kern *et al.,* 2014), survival traits analysed using threshold models yield higher heritability estimates than those analysed using linear models. Inclusion of such traits can lead to higher rates of genetic gains for longevity in selection programmes. Direct selection for longevity should nevertheless be compared with indirect selection on correlated traits expressed early in a cow's life because such traits have higher heritability (Daliri *et al.,* 2008). Indirect selection in such a scenario would also lead to faster genetic gain for longevity.

3.7   Conclusion

Heritability estimates for measures of longevity associated with survival from birth or calving were higher than for measures associated with herd or productive life. For measures of survival heritability estimates were highest in the later periods and were higher for survival from first calving than survival from birth. Survival from first calving to 96 months had the highest heritability estimate, and therefore was the most efficient in estimating genetic

variability and should therefore should be used for genetic evaluation of longevity in Sahiwal cattle in Kenya. This study has also provided part of genetic and phenotypic parameters required to include longevity in the breeding objective for the Sahiwal cattle improvement programme.

CHAPTER FOUR

EVALUATION OF THE GENETIC RELATIONSHIP BETWEEN LONGEVITY AND GROWTH, MILK YIELD AND FERTILITY TRAITS IN THE SAHIWAL BREED IN KENYA

4.1 Abstract

Direct selection for longevity results in improved health and fitness and even milk production of cows. However, longevity is lowly heritable and phenotypic information is obtained at the end of an animals life. Traits expressed early in life and which are favourably correlated to longevity can be useful in selecting for this trait. The aim of this study was to estimate genetic correlations between longevity and age at first calving, first lactation calving interval, number of services per conception, first lactation milk yield, and first parity lactation length. Heritability estimates for measures of longevity were also calculated. The measures of longevity were time between birth and last milking in days (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5). A series of five-variate animal models were fitted to estimate the nature and magnitude of genetic and phenotypic correlations between each measure of longevity and the fertility and production traits. Genetic correlations between measures of longevity and age at first calving, calving interval and number of services per conception were negative ranging from -0.14 ± 0.05 to -0.96 ± 0.06, -0.06 ± 0.03 to -0.67 ± 0.08 and -0.02 ± 0.02 to -0.73 ± 0.34, respectively. Correlations between measures of longevity and first lactation milk yield ranged from 0.88 ± 0.01 to 0.97 ± 0.03. Those with first parity lactation length ranged from -0.10 to 0.72. Long1, Long4 and Long5, which measure time between birth and last milking day, total number of days in lactation over all lactations and total milk yield over all lactations (kg), respectively, had the highest heritability estimates. These three could therefore be used to directly select for longevity. Among the traits studied, first lactation milk yield and age at first calving had the highest genetic correlation with measures of longevity. Therefore first lactation milk yield and age at first calving could therefore be used to indirectly select for longevity.

Keywords: *correlated response, fertility, genetic correlation, longevity, Sahiwal*

4.2   Introduction

Longevity or the age at which a cow leaves the breeding herd is a trait of great economic importance in dairy and beef cattle breeding (Banga *et al., 2013*). Productive longevity can also be described as the number of calvings per female (Varona *et al., 2012*). In beef and dairy cattle, longevity plays a considerable role in the farm economy by increasing the profit realised per cow and enables greater response to selection because fewer animals exit the herd due to involuntary culling (Garcia *et al.,2015*), a situation that provides greater selection intensity among females, and surplus heifers for sale (Banga *et al., 2013*).

Although milk production is considered as the single most important trait in dairy farming, cattle breeding programmes are changing their breeding objectives to include longevity and other traits (type and functional) (Banga *et al., 2013; 2014*). This enables cows to meet the challenges of high milk production. Direct selection for longevity results in improved health and fitness (Garcia *et al., 2015*) and even milk production of cows (Kern *et al., 2014a*); therefore breeding for longevity is considered to have ethical and economic benefits since it results in favorable response in profitability of beef and dairy cattle enterprises (Garcia *et al.,2015*). However, inclusion of longevity in the breeding objective is hampered because the trait is lowly heritable (Kern *et al., 2014a*; Van Pelt *et al., 2015*) and the delay in availability of phenotypic information (Lagrota *et al., 2010*), which may lead to increase in generation interval (Melo *et al., 2014*).

Availability of traits expressed early in life and which are favourably correlated to longevity can be useful in selecting for this trait. Genetic correlations between longevity and linear and fertility traits have been reported to be low to moderately positive (Zavadilová *et al., 2009b*; Van Melis *et al., 2010*; Kern *et al., 2014a*). Reproductive performance is a crucial component of culling criteria and therefore influences longevity in cattle herds and is regarded as the single most economically important trait in beef cattle. Since productive longevity is closely related to fertility, it is important to consider the genetic effects of both traits simultaneously. Despite its importance in cattle, longevity has not been studied in the Sahiwal cattle although it has been recommended for inclusion in the breed's breeding objective (Roessler *et al., 2010*; Ilatsia *et al., 2011*; Ilatsia *et al., 2012*). Estimates of genetic correlations between longevity and other performance traits, which can be used as selection criteria for longevity for the breed are also lacking.

4.3   Materials and Methods

Pedigree and performance data Sahiwal cattle in Kenya were obtained from the Sahiwal National Stud at Kenya Agricultural and Livestock Research organization (KALRO), Naivasha. A database was created by systematically entering each animal, sire and dam, date of birth and sex into a database in MSAccess. The data were checked for consistency to ensure that all animals were ordered sequentially based on date of birth such that no progeny was born before any of its parents. Also checked was presence of cyclic pedigrees (i.e. no animal appeared as both male or female) and no animal appeared as both sire and dam. The foregoing were achieved using the Animal Breeder's ToolKit (ABTK, Golden *et al.,* 1992). Measures of longevity related to productive life were: time between birth and last milking record in days (Long1), time between first calving and last milking record in days (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5). Performance data for each cow included fertility traits (Age at first calving (AFC), Calving interval (CI), first parity number of services per conception (NS)) and production traits (first lactation milk yield (FLMY) and first parity lactation length (LL))

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4.4   Data analysis

4.4.1   Estimation of the correlation between longevity and performance traits

A series of five-variate animal models were fitted to estimate nature and magnitude of genetic and phenotypic correlations between each measure of longevity and the fertility and production traits. The measures of longevity were time between birth and last milking day (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5). Fertility traits were AFC, CI, NS, while production traits included FLMY and FLL. In this model the traits were assumed to be different but correlated traits. The covariance structure of the model analyzing five traits was:

$$
G = variance \begin{bmatrix} a_1, \text{FLL} \\ a_2 \ \text{FL}MY \\ a_3 \ AFC \\ a_4 \ CI \\ a_5 \ NS \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} & g_{13} & g_{14} & g_{15} \\ & g_{22} & g_{23} & g_{24} & g_{25} \\ & & g_{33} & g_{34} & g_{35} \\ & & & g_{44} & g_{45} \\ symm & & & & g_{55} \end{bmatrix} \otimes A = G_0 \otimes A
$$

where G_0 is the genetic (co)variance matrix between animal effects; $\otimes$ =Kronecker product and A =numerator relationship matrix among animals. The residual variance among record of different traits was assumed to zero; g_{ii} is the variance for trait i and g_{ij} is the covariance between any two traits, i and j.

4.4.2 Genetic correlation

Genetic correlation between two traits i and j, $r_{g_{i,j}}$ was estimated as:

$$r_{g_{i,j}} = \frac{\sigma_{i,j}}{\left(\sigma_{ii}^2 . \sigma_{jj}^2\right)^{0.5}}$$

where $\sigma_{i,j}$ σ_{ii}^2 and σ_{jj}^2 are the covariance between traits i and j, variance of trait i and j, respectively.

4.5   Results and discussion

Means and standard deviations for selection criteria for measures of longevity are given in Table 4.6. Heritability estimates for measures of longevity from multivariate analysis were generally higher than those from univariate analysis. This could be due to the additional information from correlated traits in multivariate analysis (Mrode, 2014). The mean values for measures of longevity from birth and first calving were similar to those reported by Kern *et al.* (2014) for Brazilian Holsteins and Nilforooshan and Edriss (2004) who reported values ranging from 57.2 months and 30.1 months for Long1 and Long2 respectively. For Brazillian Holsteins, Kern *et al.* (2015) reported values of 60 and 33 months, respectively.

Long5 or milk production in all lactations is an indicator of a cows delay to involuntary culling. With increased milk production culling is based preferentially on production leading to higher proportion of cows in a herd with higher productive capacity and longer herd life. Average for Long3 of 1.5 was lower than values of 2.7 and 2.8 reported for Brazilian and US Holsteins, respectively (Tsurata *et al.,* 2005; Kern *et al.,* 2015). Higher values of 3.0 and 2.4

Table 4.6: Means, standard deviations, minimum and maximum for longevity measures related to productive life for Sahiwal cattle in Kenya

Measure	Mean	Standard deviation	Minimum	Maximum
Long1, days	2231.1	887.8	960.0	6246.0
Long2, days	1172.7	703.7	226.0	4720.0
Long3, count	2.7	1.4	1.0	11.0
Long4, days	738.0	428.4	10.0	3147.0
Long5, kg	3425.5	3534.2	10.0	11616.0

Longevity was defined as time between birth and last milking day (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5)

for Slovak Holsteins and Simmental dairy cows, respectively, have been reported (Potocnik *et al.,* 2011; Strapák *et al.,* 2011). In the Kenyan Sahiwal herd, cows remained on average 2231.1 days, 1172.7 days from birth (Long1) or first calving (Long2), respectively, an average of 738 days in milk till they exited the herd through death or culling. An increase in total days in milk, cows are expected to produce more milk, accompanied by a lower occurrence of reproductive, udder and conformation problems (Cruickshank *et al.,* 2002). Mean values of Long1 (74.4months) and Long2 (39.1 months) were higher than those reported for Brazilian Holsteins (60 and 33 months, respectively) and 57.2 months and 30.1 months, respectively reported by Nilforooshian and Edriss (2004). The higher values reported in the current study could be due breed differences, where exotic dairy breeds in temperate and tropical climatic conditions have been shown to exit herds earlier due to involuntary culling (Sewalem *et al.,* 2010) compared to the zebu.

Estimates of components of additive genetic and residual variances for measures of longevity related to productive life are shown in Table 4.7. Additive genetic variances ranged from 0.06 (Long3) to 366,033 (Long5). Corresponding heritability estimates were low, with the highest being 0.097± 0.04 (Long5).All measures of longevity had high estimates of residual variances and low estimates of additive genetic variance hence the low estimates of

heritability. The heritability estimates found in the current study of 0.08 to 0.10 were within the range reported for different cattle populations under tropical conditions of 0.06 to 0.18 (Kern *et al.,* 2014; M'hamdi *et al.,* 2014). Heritability estimates cattle populations in temperate climatic conditions ranged from 0.02 to 0.10 (Vollema and Groen 1996; Tsurata *et al.,* 2005). The low heritability estimates for measures of longevity from linear models yield lower estimates compared to survival models partly due to inclusion of censored records and time-dependent variables (Ducrocq *et al.,* 1988; Forabosco *et al.,* 2006) since the environmental conditions affecting cow survival changes over time.

Table 4.7: Estimates of additive genetic variance (σ_a^2), residual (σ_e^2) and heritability estimates (h^2) for measures of longevity from multivariate analyses for the Sahiwal cattle in Kenya

Parameter	Long1	Long2	Long3	Long4	Long5
σ_a^2	24121.1	28761.1	0.11	5595.0	398380.2
σ_e^2	312591.0	319900.1	1.50	127280.1	3811821.3
h^2	0.07 ±0.08	0.08±0.01	0.07±0.02	0.04±0.02	0.09±0.01

Longevity was defined as time between birth and last milking day (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5)

Co-variance components, heritability estimates and genetic correlations between selection criteria and measures of longevity are given in Table 4.8. The heritability estimates for measures of longevity were low, ranging from 0.03 to 0.13 (Table 4.8). This indicates that longevity is influenced more by environmental factors, meaning that direct selection for these traits would yield low genetic gains. Other studies which reported low heritability estimates include Kern *et al.* (2015) who reported estimates ranging from 0.05 to 0.07. For traits expressed early in life relative to the measures of longevity in the current study, first lactation milk yield had the highest heritability estimate, ranging from 0.12 to 0.23 followed by first parity lactation length (0.07 to 0.12) (Table 4.8).

Table 4.8: Co-variance components, heritability and genetic correlations between measures of longevity and performance traits for Sahiwal cattle in Kenya

Longevity	Performance trait	σ^2_a	σ^2_e	$h^2 \pm se$	$\sigma_{1,2}$	r_g
Long1		24121.1	312591.0	0.07±0.08		
	Age at first calving, mo	1.8	21.4	0.08±0.01	-58	-0.28±0.06
	First parity calving interval, days	209.9	15002.0	0.01±0.01	-3498.7	-0.67±0.08
	First parity lactation length, days	10147.0	91570.1	0.10±0.06	-1634.1	-0.10±0.06
	First parity milk yield	43565.9	190761.0	0.19±0.02	31490.0	0.97±0.03
	First parity services/conception,	0.07	2.7	0.02±0.03	-0.63	-0.02±0.02
Long2		28761.1	319900.1	0.08±0.01		
	Age at first calving, mo	1.97	22.70	0.08±0.02	-54.2	-0.14±0.05
	First parity calving interval, days	739.8	14821.1	0.05±0.04	-1853.4	-0.24±0.04
	First parity lactation length, days	2463.2	18347.1	0.12±0.03	6065.1	0.72±0.03
	First parity milk yield	49277.0	210931.1	0.19±0.02	36473.0	0.97±0.04
	First parity services/conception,	0.093	2.49	0.04±0.03	-41.9	-0.18±0.14
Long3		0.11	1.50	0.07±0.02		
	Age at first calving, mo	1.29	11.6	0.10±0.02	-0.36	-0.96±0.06
	First parity calving interval, days	215.6	15672.0	0.01±0.02	-0.78	-0.16±0.08
	First parity lactation length, days	9170.63	91824.2	0.10±0.03	2.56	0.08±0.19
	First parity milk yield	49121.1	166000.1	0.23±0.04	68.6	0.93±0.06
	First parity services/conception,	0.03	2.43	0.01±0.01	-0.04	-0.70±0.18
Long4		5595.0	127280.1	0.04±0.02		
	Age at first calving, mo	1.2	27.3	0.04±0.02	-69.5	-0.85±0.08
	First parity calving interval, days	323.4	15033.1	0.02±0.03	-168.8	-0.13±0.07
	First parity lactation length, days	10543.0	82951.1	0.11±0.02	1761.0	0.23±0.04
	First parity milk yield	33851.0	217541.0	0.13±0.01	12063.1	0.88±0.01
	First parity services/conception,	0.03	2.4	0.01±0.09	-9.4	-0.73±0.34
Long5		398380.2	3811821.3	0.09±0.01		
	Age at first calving, mo	1.4	12.0	0.10±0.01	-121.2	-0.16±0.03
	First parity calving interval, days	341.2	12037	0.03±0.02	-699.3	-0.06±0.03
	First parity lactation length, days	165.2	2054.2	0.07±0.02	2731.0	0.37±0.02
	First parity milk yield	6110.2	208386.0	0.18±0.01	129339.1	0.95±0.05
	First parity services/conception,	0.04	2.4	0.02±0.01	-70.5	-0.55±0.06

Longevity was defined as time between birth and last milking day (Long1), time between first calving and last milking record in months (Long2), number of lactations initiated (Long3), and total number of days in lactation over all lactations (Long4), total milk yield over all lactations (kg) (Long5)

Lower heritability estimates were obtained for first parity calving interval (0.01 to 0.05) and number of services per conception (0.01 to 0.04). Among the fertility traits, age at first calving had higher heritability estimates, ranging from 0.04 to 0.10.

Genetic correlations between fertility traits and measures of longevity were negative ranging from -0.02 to -0.95. This indicates that cows with long first lactation CI, and which calved first later or required more services per conception were less likely to remain in the productive herd. Studies which have reported similar negative correlations include Sewalem *et al.* (2008). In this study, cows that required more services per conception or had longer calving intervals were at greater risk of being culled. Similar results were reported for French Holsteins by Beaudeau *et al.* (1994). Zavadilová, and Štípková (2013) reported that cows with higher age at first calving tended to have shorter length of productive life and were associated with a higher risk of being culled (Sewalem *et al.,* 2005b). Thus selecting for earlier age at first calving will lead to an increase in longevity, apart from shortening generation interval (Pirlo *et al.,* 2000) and decreasing replacement expenses (Gardner *et al.,* 1988). In general, late first calving in cows is associated with fertility and health problems, which may be exhibited in the entire life of a cow (Nilforooshan and Edriss, 2004; Páchová *et al.,* 2005; Zavadilová, and Štípková, 2013). Genetic correlations between measures of longevity and first lactation milk yield and lactation length were positive and moderate to high, and ranged from 0.41 to 0.99. However, heritability estimates of fertility traits were close to 0, as found in the current study and in literature (Zink *et al.,* 2012; Albarrán-Portillo and Pollott, 2013).

4.6   Conclusion

Long1, Long3, Long4 and Long5, which measure time between birth and last milking day, number of lactations initiated, total number of days in lactation over all lactations and total milk yield over all lactations (kg), respectively, had the highest heritability estimates. These two could therefore be used to directly select for longevity. The genetic correlations between Long1 and Long5 and FLMY and AFC were high and positive and negative, respectively. Therefore selecting for more FLMY and shorter AFC would lead to correlated increase longevity. As such FLMY and AFC could therefore be used to indirectly select for longevity.

CHAPTER FIVE

EVALUATION OF EFFECT OF INBREEDING ON TRAITS OF ECONOMIC IMPORTANCE IN KENYA SAHIWAL CATTLE

5.1   Abstract

Pedigree and performance data for the Sahiwal cattle from the National Sahiwal Stud (NSS) in Kenya were used to evaluate the effect of inbreeding on first lactation milk yield (FLMY), age at first calving (AFC), calving interval (CI), and lactation length (LL). These traits were analysed using a univariate animal model without fitting effect of inbreeding to generate a vector of errors. Effects of inbreeding on the traits were determined by fitting four regression models (linear, quadratic, exponential and Michaelis-Menten) to the errors generated by the animal model. The linear, exponential and Michaelis-Menten models were significant ($P < 0.05$) for all the studied traits while the quadratic model was only significant ($P < 0.05$) for calving interval. Inbreeding had a positive effect on calving interval, age at first calving, and lactation length, shortening calving both interval and age at first calving and increasing lactation length. The relation between inbreeding and depression of traits was not linear, with greater depression after 15% inbreeding. Genetic evaluation of the Kenyan Sahiwal should account for inbreeding. The results of the current study indicate the need to consider effect of inbreeding on traits of economic importance for the Sahiwal cattle breed when carrying out genetic evaluations. The mating plan for the NSS should be designed so as to control future rates of inbreeding while achieving genetic gain.

Key words: *Genetic gain, inbreeding depression, Kenya, Optimum contribution, Sahiwal*

5.2   Introduction

Increase in inbreeding leads to reduced genetic variability by reducing heterozygosity over many loci (Falconer and Mackay, 1996), increased risk of breeding programmes due to variance of genetic gains (Meuwissen, 1991). Increase in inbreeding also leads to increased risk of emergence of lethal recessive homozygous alleles (König and Simianer, 2006). A more immediate concern to dairy farmers is the reduction of performance of inbred animals, referred to as inbreeding depression due to inbreeding (Falconer and Mackay, 1996).

For the Kenya Sahiwal population, Muasya *et al.* (2011) reported a gradual increase in inbred animals from 0 in 1967 to 80% in 2008 with a corresponding increase in mean individual inbreeding coefficient from 0 to about 2.5% in 2008. The proportion of inbred animals increased rapidly from 1% to about 98% in the most recent complete generation. As the proportion of inbred animals increase reduction of inbreeding through pairing of mates that are less related than the average in the population becomes difficult (Thompson *et al.,* 2000). In the Kenyan Sahiwal cattle, inbreeding level increased from 1.2 to 2% as the proportion of inbred individuals increased (Muasya *et al.,* 2011). Other studies have reported various estimates of inbreeding for zebu the Sahiwal breed. In Nicaraguan inbreeding level of 13.0% has been reported for Creole cattle breed (Corrales *et al.,* 2010). Among the Nelorre, Guzerat and Gyr zebu cattle breeds in Brazil, inbreeding levels ranging from 1.8 to 2.8% have been reported (Filho *et al.,* 2010; Faria *et al.,* 2009).

Inbreeding depression decreases cow survival, reproductive performance and milk production and increases rate of disposal or loss of replacement heifers before first calving, age at puberty through reduced growth (Du Toit *et al.,* 2012). Every 1% increase in inbreeding leads to a 10 kg of milk to 26kg decline in milk production per lactation (Mostert, 2011) and decrease of about 13 days in productive life (CDN, 2008; Smith *et al.,* 1998). Du Toit *et al.* (2012) a similar effect of inbreeding on functional herd life in Jersey cattle. Cows with high inbreeding level have also been reported to have a higher risk of being culled (Rokouei *et al.,* 2010). Inbreeding depression depends not only on actual level of inbreeding but also on the rate of inbreeding such that animals with the same level of inbreeding may have different inbreeding depression effects depending on the completeness of their respective pedigrees (González-Recio *et al.,* 2007; Gutiérrez *et al.,* 2009). The quality of pedigree can be accounted for by estimating the rate of inbreeding (Gonzalez-Recio *et al.,* 2007) which

indicates the increment in inbreeding regardless of number of known generations in an individual's pedigree (Gonzalez-Recio *et al.,*2007). The objective of the study was therefore to evaluate the effect of inbreeding on lactation milk yield, lactation length and fertility traits in the Kenyan Sahiwal cattle population.

5.3   Materials and Methods

5.3.1   Description of the study sites and data collection

Pedigree data for the Sahiwal cattle in Kenya were obtained from the Sahiwal National Stud at Kenya Agriculture and Livestock Research Organization (KALRO), Naivasha. A database was created by systematically entering each animal, sire and dam, date of birth and sex into a database. The data were checked for consistency to ensure that all animals were ordered sequentially based on date of birth such that no progeny was born before any of its parents and that there were no cyclic pedigrees (i.e. no animal appeared as both male or female) and no animal appears as both sire and dam using the Animal Breeder's Tool Kit (ABTK, Golden *et al.,* 1992). Data on Lactation milk yield for the first lactation (LMY), lactation length (LL), Calving interval (CI) and Age at first calving (AFC) were added onto the pedigree database of each animal. Age at first calving was derived as the interval in days from date of birth to first calving. Calving interval was derived as the interval between consecutive calvings for the first three lactations. Means, standard deviations (SD) and coefficients of variation (CV %) for lactation milk yield (LMY), Lactation length (LL), age at first calving (AFC) and calving interval (CI) are given in Table 5.9.

Table 5.9: Descriptive statistics of lactation milk yield (LMY), age at first calving (AFC), calving interval (CI) and lactation length (LL)

Trait	No. of records	Mean	SD
FLMY, kg	1841	1287.9	509.6
AFC, mo	1767	44.1	7.2
CI, days	1841	474.5	125.5
LL, days	1837	287.1	50.7

The large CV% for FLMY reflects the great variation between individual cows in these traits. Similar results were reported for Egyptian buffalos (Khatab *et al.,* 2007).

5.3.2 Assessment of level of inbreeding

The inbreeding coefficient (F_i) for each individual in the pedigree was calculated as the probability that two alleles are identical by descent according to the method of Van Raden (1992). This method makes it possible to compute the inbreeding coefficients per generation, and assumes that founders are inbred or related, an assumption which is important when pedigrees are heterogeneous. The inbreeding coefficient of an individual with unknown origin (founder) is equal to half the average genetic relationship between genetic groups of its phantom parents.

5.3.3 Estimation of (co)variances and estimated breeding values

Estimates of variance and estimated breeding values were obtained by performing univariate analyses on first lactation milk yield (LMY), lactation length (LL), Age at first calving (AFC) and calving interval (CI) using the following animal model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}$$

where y is a vector of observations for LMY, LL, AFC and CI in each lactation, **b** and **a** and **e** are vector of fixed, random animal effects, and random residuals, respectively and **X** and **Z** are the incidence matrices relating fixed and random animal effects to observations, respectively. The random effects will be assumed to be normally distributed with a mean=0 and variance as follows: $\mathbf{a} \sim \mathbf{N}\left(\mathbf{0}, \mathbf{A}\sigma_a^2\right)$ and $\mathbf{a} \sim \mathbf{N}\left(\mathbf{0}, \mathbf{I}\sigma_e^2\right)$, where σ_a^2 and σ_e^2 are animal and residual variances, respectively, and **A** and **I** are the numerator relationship and identity matrices, respectively. The models for FLMY, CI and LL included fixed effects of year season of calving and age at calving. A similar model was used for AFC but with year season of birth instead of year season of calving. Variance covariance components for the traits under study were estimated using MTDFREML software package (Boldman *et al.,* 1995).

Analysis of pedigree, inbreeding coefficient (F) and equivalent complete generations were estimated using ENDOG version 4.5 computer programme (Gutiérrez and Goyache, 2005). Equivalent complete generations were estimated as:

$$\mathrm{ECG} = \left(\frac{1}{2}\right)^n$$

where n is the number of generations separating each individual from each known ancestor (Maignel *et al.,* 1996). Inbreeding coefficient (F) was computed after Meuwissen and Luo (1992). Rate of inbreeding (ΔF) was calculated for each generation as:

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$$ where F_t and F_{t-1} are the average inbreeding at t^{th} generation. Only animals with ECG of at least 1.5 were included in the analysis of F (2367 animals). The limit for ECG was imposed to ensure that ΔF was estimated as accurately as possible.

5.3.4   Estimation of inbreeding depression

A vector of errors. e_i for each trait were generated from univariate analysis using WOMBAT (Meyer, 2007) as follows;

$$e_i = X_i\beta - Z_i a$$

The effect of inbreeding on the traits studied was determined by fitting the followingfour regression models:

Linear, $e_i = \beta_0 + \beta_1(F_i - \bar{F}) + \varepsilon_i$

Quadratic, $e_i = \beta_0 + \beta_1\left(F_i - \bar{F}\right) + \beta_2\left(F_i - \bar{F}\right)^2 + \varepsilon_i$,

Exponential, $e_i = \beta^{F_i} + \varepsilon_i$ and

Michaelis-Menten $e_i = \dfrac{\beta_1\left(1 - F_i\right)}{\beta_2 + \left(1 - F_i\right)} + \varepsilon_i$ around the errors, where β_0 and β_i are the intercept and slope parameters, respectively. For the Michaelis-Menten model, β_1 is the maximum rate of inbreeding, while β_2 is the level of the response variable (trait) at which the rate of inbreeding is half of the maximum The model of the analyses was $e_i = \Phi(F_i) + \varepsilon$, where $\Phi(F_i)$ is the regression function on inbreeding efficient of an animal *i* and ε represents the deviations of the errors from the predicted errors in the regression function.

5.4   Results and Discussion

Summary of number of animals, mean inbreeding levels by groups of birth year and number of animals in each inbreeding class is shown in Table 5.10. In the 1965-1974 birth year group 79% of the animals were not inbred, while in the last year group only 11% were non-inbred. Mean inbreeding level across the year of birth groups increased from 0.9 to 1.6%. A similar trend has been reported in Jersey cattle in South Africa (Du Toit *et al.,* 2012). The mean inbreeding level and annual rate of inbreeding for the population studied were 0.7 and 0.33%, respectively. Higher average inbreeding levels of 15% in Guzerat cattle (Panetto *et al.,* 2010),

1.75 to 2.28% in Brazilian zebu cattle (Faria *et al.,* 2009), 1.73% in the Nellore breed (Britto *et al.,* 2013) have been reported. Rates of increase in inbreeding lower than that reported in the current study ranging from 0.04 to 0.08% have been reported among dairy cattle breeds in Canada (CDN, 2010).

Table 5.10: Number of animals, mean inbreeding (%F) by birth year group and distribution of animals in each inbreeding class for cows used in analysis

Birth year	No. Animals	% Inbred	Mean F%
1965-1974	732	11.1	0.9
1975-1984	733	12.1	1.0
1985-1994	480	50.8	1.5
1994-2008	422	78.8	1.6

The general increase in inbreeding among the cows in the current study could be linked to intense use of a small number of superior sires and more complete pedigree information in more recent years (Muasya *et al.,* 2011).

Table 5.11: Least square means (se) of the effect of inbreeding coefficients on Lactation milk yield (LMY), age at first calving (AFC), calving interval (CI) and lactation length (LL)

Inbreeding coefficient	No. of animals	LMY, kg	LL, days	AFC, days	CI, days
Zero	2015	1227.9 (15.3)[a]	287.4(1.4)[a]	1387.8(5.3)[a]	474.2[a]
>2.25	352	970.4 (128.9)[b]	283.8(11.5)[a]	1388.3(43.6)[a]	538.4[b]

Means with different superscripts are different at 5% level of significance

For FLMY, non-inbred animals produced significantly higher milk yield and longer CI (P<0.05) compared to inbreds. For the other traits, non-inbred animals performed better than inbred animals, though the means were not significantly different (P>0.05). The depression in performance or inbreeding depression is attributed to inbreeding depression is caused by increased homozygosity of individuals. Increased homozygosity lowers fitness through

increase in the frequency of homozygous recessive detrimental mutations, and increased homozygosity for alleles at loci with heterozygote advantage (Griffiths *et al.* 1999; Charlesworth and Willis 2009). There is emerging evidence that lowly heritable traits such as fertility (e.g. CI, AFC) exhibit more depression due to inbreeding because of their low genetic variation (Kristensen *et al.* 2005), though results from the current study showed significant depression in FLMY only (Table 5.11). Effect of inbreeding on the traits studied is shown in Table5.12. The linear, Exponential and Michaelis-Menten models were significant (P<0.05) for all traits studied (Table 5.12).

Table 5.12: Estimates of the inbreeding regression coefficients for first lactation milk yield (FLMY), lactation length (LL), calving interval (CI) and age at first calving (AFC) for the Kenyan Sahiwal cattle

	Models			
	Linear	Quadratic	Exponential	Michaelis-Menten
FLMY (kg)	-16.7*	-0.42ns	0.74**	-0.198***
LL (days)	15.17*	0.33ns	1.02*	-0.48***
CI (days)	-13.47*	-0.09*	1.45**	0.23***
AFC (mo)	-0.18*	-0.05ns	0.95*	0.06***

*ns=not significant, *=P<0.05; **=P<0.01; ***P<0.001*

The quadratic model was significant (P<0.05) for CI only. Carrillo and Siewerdt (2010) and Mahlado *et al.* (2013) reported a similar pattern, where the linear, exponential and Michaelis-Menten models were significant for all traits studied, whereas the quadratic model was not

Table 5.13: Error means square from linear, exponential and Michaelis-Menten on first lactation milk yield (FLMY), lactation length (LL), age at first calving (AFC) and calving interval (CI)

	Linear	Quadratic	Exponential	Michaelis-Menten
First lactation Milk yield	120574.8	120615.6	120625.2	120313.1
Lactation length	594.9	597.5	595.5	579.0
Calving interval	7459.8	7438.0	7434.0	7489.0

significant for any trait studied. The residual variances for the three models were similar (Table 5.13) implying equivalence in goodness of fit. The lack of significance for the quadratic model could be due to the fact that it assumes the effect of inbreeding would decline after reaching a peak (Mahlado *et al.*, 2013). From the results of the current study and that of Mahlado *et al.* (2013) it is emerging that inbreeding depression increases with increase in inbreeding level.

Similar results were reported by Carrillo and Siewerdt (2010) and Mahlado *et al.* (2013), meaning that any of the three models would be adequate in estimating inbreeding depression. Of these models, the linear model, which is easy to fit and the fact that its parameters have direct interpretation, would suffice. However, its limitations were its lack of flexibility and its inability to cope with departure from linearity at higher inbreeding levels (Fig. 1). The increase in inbreeding led to a decrease in first lactation milk yield, calving interval and age at first calving (Fig. 1) implying a depression in milk yield but an improvement in CI and AFC.
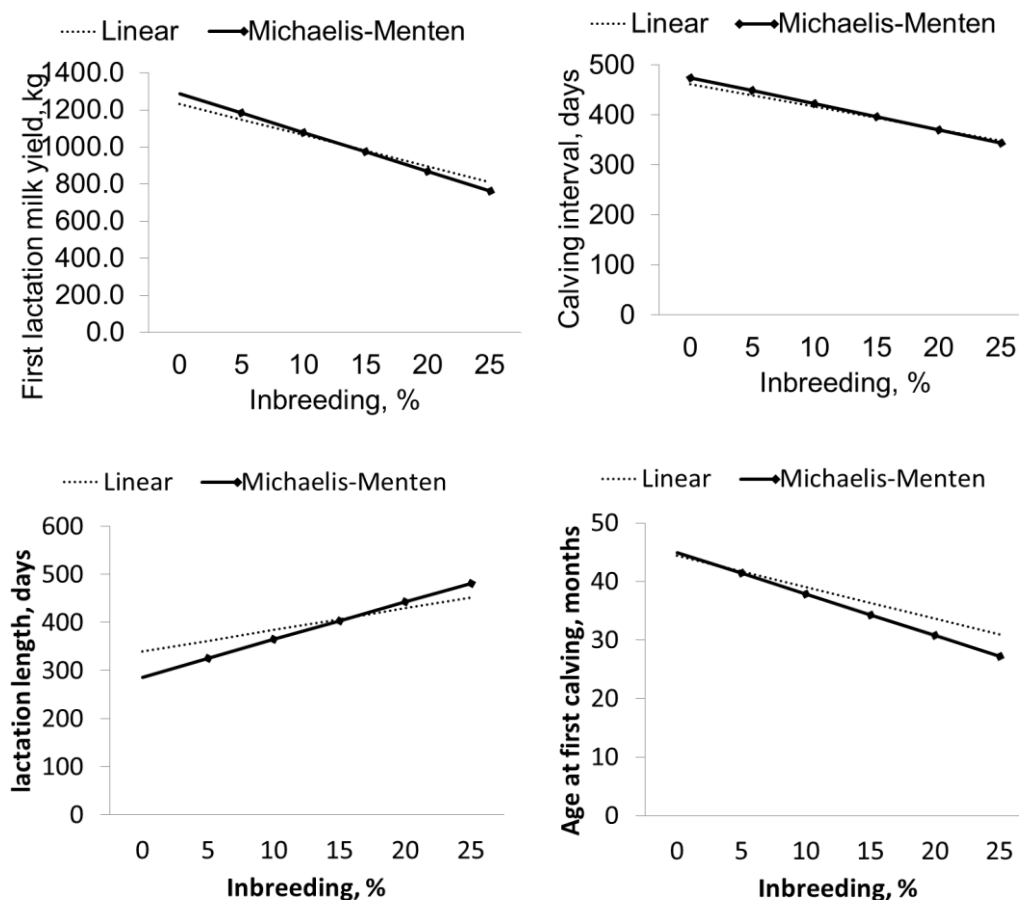

Figure 1: Effects of inbreeding depression on first lactation milk yield, calving interval, lactation length and age at first calving

Similar findings have been reported in previous studies. Mahlado *et al.* (2013) found that the exponential and the Michaelis-Menten models were significant for all traits studied. However, unlike in the current study, the exponential model was not significant for any of the traits studied. In the current study, for inbreeding levels up to 0.15, inbreeding was approximately linear. Beyond this level of inbreeding, there seemed to be a higher inbreeding depression in all traits (Fig. 1). Similar results have been reported by Mahlado *et al.* (2013) and Santana Jûnior *et al.* (2011). In the study by Santana Junior, animals with an average F=25% produced less milk by 107kg compared to non inbreds. In the current study, inbred animals (F=15%) had a depression in milk production of 258 kg in the first lactation. For the study by Mahlado *et al.* (2013) at an average F=0.25, animals produced 50.4kg less. Others who have reported a decline in milk yield due to increase in inbreeding include Panetto *et al.* (2010) who found a reduction of 15.25kg in milk yield in Guzerat cattle when half sibs were mated. In populations with higher inbreeding levels (12.5%), high inbreeding depression for milk yield ranging from 345 to 480 kg among Holstein cows translating to 27.6 kg to 38.4 kg per 1% increase in inbreeding have been reported (Smith *et al.,* 1998; Thompson *et al.,* 2000). Other studies have found a non-linear relationship between inbreeding and milk yield resulting in a depression of 380 kg in 305 day milk yield among highly inbred cows (F=12.5%) (Gulisija *et al.,* 2007). For cows with a similar inbreeding level, Maiwashe *et al.* (2008) reported decline of 170kg in 305 milk yield. Panetto *et al.* (2010) reported a positive effect of inbreeding on daily milk yield, contrary to that reported in the current study. Among Buffaloes in Brazil, Santana Junior *et al.* (2011) reported a decrease of 4.3kg while Malhado *et al.* (2013) found a value of 14.8kg for 1% increase in inbreeding, whereas Mirhabibi *et al.* (2007) reported a decrease of 18.2kg.

Lactation length deteriorated by 0.3 days per 1% increase in inbreeding, though the effects were not significant (P<0.05). To the contrary, inbred animals had slightly better fertility compared to non-inbreds (Table 5). Similar to the current study, Malhado *et al.* (2013) found a favourable relationship between inbreeding and AFC among Brazilian Buffaloes. In this study, a 1% increase in inbreeding led to a shortening of AFC by 0.76 days. Thompson *et al.* (2000) reported that low to moderate levels of inbreeding (F<0.07) reduced AFC by 3 to 5 days compared to non-inbred animals. Contrary to the positive effects of inbreeding on CI and AFC reported in the current study, Panetto *et al.* (2010) found that these traits increased by up to 14 day and 11 days for every 1% increase in inbreeding in a Guzerat dairy herd.

Other studies reported increase in CI and AFC. Hudson and Van Vleck (1984) reported an expected increase in CI by 2 day whereas AFC was expected to increase by 0.4 days for every 1% increase in inbreeding. Among Irish Holstein-Friesian cows, McParland *et al.* (2007) reported that mating between half-sibs (F=12.5%) would result in an increase in AFC and CI of 2.5 days and 8.8 days, or 0.2 and 0.7 days per 1% increase in inbreeding, respectively. A smaller effect of inbreeding depression of 0.263 days on CI was reported for Alentejana cattle (Carolino and Gama, 2008). Other studies that have reported a decline in fertility due to inbreeding include González-Recio *et al.* (2007), Malhado *et al.* (2013). In Iranian Holstein cattle, Rokouei *et al.* (2010) reported a non-significant effect of inbreeding on CI in first and second lactations.

5.5   Conclusion

Inbreeding had deleterious effect in performance on the traits studied. The relation between inbreeding and depression of traits was not linear, with greater depression after 15% inbreeding. Genetic evaluation of the Sahiwal cattle in Kenya should account for inbreeding. Matings should be planned in order to check future increase in inbreeding while achieving acceptable rate of genetic progress in the programme's breeding goal.

CHAPTER SIX

GENERAL DISCUSSION

6.1Aim of the study

Direct selection for longevity results in improved health and fitness (Garcia *et al.,* 2015) and even milk production of cows (Kern *et al.,* 2014a); therefore breeding for longevity is considered to have ethical and economic benefits since it results in favorable response in profitability of beef and dairy cattle enterprises (Garcia *et al.,*2015). Many breeding programmes across the world have therefore begun to recognize the economic importance of longevity and have estimated genetic parameters for longevity and included the trait in breeding objective (Forabosco *et al.,* 2009; Banga *et al.,* 2013: 2014; Interbull, 2015). Inclusion of longevity in the breeding objective is hampered because the trait is lowly heritable (Kern *et al.,* 2014a; Van Pelt *et al.,* 2015) and the delay in availability of phenotypic information (Lagrota *et al.,* 2010). Traits expressed early in life and which are favourably correlated with longevity can be used as selection criteria (Van Melis *et al.,* 2010). However, genetic correlations between longevity and fertility, growth and milk yield traits have not been estimated for the Kenyan Sahiwal population. ; Ilatsia *et al.,* 2011).

Genetic improvement of the Sahiwal in Kenya breed is carried out under a closed nucleus breeding program (CNBP). Closed nucleus breeding programmes are associated with high inbreeding levels and low effective population sizes due to increased focus on a few high performing often closely related animals (Fernandez *et al.,* 2011; Mwangi *et al.,* 2015). Longevity, milk yield and reproductive performance and milk yield have been shown to decrease while, rate of disposal or loss of replacement heifers before first calving, age at puberty increased due to inbreeding through reduced growth (du Toit *et al.,*2012). For every increase of 1% in inbreeding, productive life has been reported to decrease by about 13 days (CDN, 2008). Cows with high inbreeding level have also been reported to have a higher risk of being culled (Rokouei *et al.,* 2010), reduced reproductive efficiency and stayability. The objectives of this study were to (i) estimate genetic and phenotypic parameters for longevity (ii) to estimate genetic relationship between longevity and milk yield and fertility traits and (iii) to determine the effect of inbreeding on traits of economic importance in the Kenyan Sahiwal population.

This thesis addressed three research questions namely; (i) What are the variance components, genetic and phenotypic parameters for longevity in the Kenyan Sahiwal population? (ii) What is genetic relationship between longevity and growth, milk yield and fertility traits in the Kenyan Sahiwal population? and What is the effect of inbreeding on longevity, first lactation milk yield and fertility traits in the Kenyan Sahiwal population?

6.2 Study Methodology

Measures of longevity related to productive life i.e. were defined alternatively as time between birth and last milking record in days (Long1), length of productive life or functional longevity (days) (Long2), number of lactations initiated (Long3), total number of days in lactation over all lactations (Long4) and total milk yield over all lactations, kg (Long5) (Kern et al 2014). Variance components, genetic and phenotypic parameters for longevity were estimated using a linear model using the expectation maximization method in WOMBAT (Meyer 2007) using a convergence criterion of 10^{-9}. Measures of longevity related to survival (survival from birth to 44 months (Long6_44), 56 months (Long6_56), 80 months (Long6_80), 92 months (Long6_92), 104 months (Long6_104), and 128 months (Long6_128) and survival from first calving as survival from for 12 months (Long7_12), 36 (Long7_36), 60 (Long7_60), 84 (long7_84) and 96 months (Long7_96) from first calving) were analysed as threshold traits assumed to have an underlying continuous distribution.

The threshold model relates survival to a given age in a categorical scale with a normal underlying continuous scale. Variance components for survival measures were estimated via Bayesian inference using THRGIBBS1F90 (Misztal *et al* 2002). Outputs from this software were used to obtain a posteriori estimates using POSTGIBBSF90 (Misztal *et al* 2002). Convergence of all Bayesian analyses were verified using the R program using Geweke's (1992) and Heidelberger and Welch (1983) diagnostics, from the Bayesian Output Analysis Program – BOA (Smith 2005).

The second objective estimated genetic correlations between longevity and fertility and milk yield and lactation length in the first lactation. Genetic correlations between each measure of longevity (Long1, Long2, Long3, Long4 and Long5) and age at first calving, first parity

services per conception, calving interval, milk yield and lactation were estimated through a series five-variate analyses via a linear model.

The third objective dealt with assessing the effect of inbreeding on traits of economic importance. Effects of inbreeding on the traits were determined by fitting four regression models (linear, quadratic, exponential and Michaelis-Menten) to the errors generated by the animal model. The inbreeding coefficient (Fi) for each individual in the pedigree was calculated as the probability that two alleles are identical by descent according to the method of VanRaden (1992). Estimates of variance and estimated breeding values were obtained by performing univariate analyses on first lactation milk yield (LMY), lactation length (LL), Age at first calving (AFC) and calving interval (CI) using the following a univariate animal model using WOMBAT software (Meyer *et al.,* 2007). Analysis of pedigree, inbreeding coefficient (F) and equivalent complete generations were estimated using ENDOG version 4.5 computer programme (Gutiérrez and Goyache, 2005). The linear, quadratic and Michaelis-Menten models were fitted to the vector of errors for each trait generated from the univariate analysis.

The first step in inclusion of a trait in the breeding objective of a given breeding programme entails estimation of genetic and phenotypic parameters, its correlation with other traits of economic importance and to quantify the effect of inbreeding on the trait(s) especially for closed nucleus breeding programmes. This study was carried out to provide genetic and phenotypic parameters for longevity, its correlation with other traits in the breeding objective of the Kenyan Sahiwal cattle and to estimate inbreeding depression for traits of economic importance

6.3.   Genetic parameters

Genetic parameters for measures of longevity related to productive life or survival were estimated using linear and threshold models, respectively. Estimates of heritability for longevity measures estimated using threshold models (survival measures) were higher than those estimated using linear models (measures related to productive life). Long7_96 had highest additive genetic variance and heritability estimate, and therefore should be used for genetic evaluation of longevity in Sahiwal cattle in Kenya.

Longevity is quite important in dairy and beef cattle herds from an economic, herd-health and animal welfare point of view. Intensive selection for production and reproduction traits without considering functional and type traits leads to decreased longevity (Engblom *et al.*, 2008; Knaus, 2009). In the current study the estimates of additive genetic variances and heritabilities were significantly different from 0 based on their 95% confidence intervals. Similar results were reported by Mezsros *et al.* (2010). The 95% confidence intervals were also wide. Heritability estimates for measures of longevity are dependent on breed (Kern et al., 2017) and method of analysis (Mezsros *et al.*, 2010) and definition of longevity (Kern et al 2014a,b; Van Pelt et al., 2015). In general heritability estimates of longevity are low regardless of method of evaluation, breed or species (Mezsros *et al.*, 2010; Kern *et al.*, 2014a,b; Van Pelt *et al.*, 2015). However, given the immense economic importance of this trait it is worthwhile to consider it as a selection criterion in cattle breeding. The benefits of increased longevity are numerous. Longer productive life means lower replacement and treatment costs associated with reproductive and animal health disorders, feet, udder and other functional traits (Ducrocq *et al.*, 1988; Essl, 1998; Forabosco *et al.*, 2009). Because of this countries are changing the breeding objectives for dairy and beef cattle to include longevity. For instance by 2014, 12 countries included longevity in national genetic evaluations either as a single trait analysed through survival analysis or in a multiple trait model (Interbull, 2015). Further, Evaluation of sires for functional longevity in breeding programmes is very vital because it would complement estimated breeding values for production traits (Ducrocq, 1998).

The measures of longevity used in the current study relate to function longevity which is defined as the ability to delay involuntary culling due to factors other than production (lameness, fertility problems, mastitis, or other diseases). For instance, survival to predefined ages as used in the current study captures information on culling early in life which has the most detrimental effect on herd profitability. Milk production is deemed the single most important factor affecting productive life due to its direct effect on herd profitability. Cows in low milk production classes have a higher relative risk of being culled (Ducrocq *et al.*, 1994).

Although it was not considered in the current study, voluntary selection for milk components influences cow risk of being culled. Cows with low protein and fat percentage have higher risk of being culled (Kern et al., 2016). These results are similar to those reported by Sewalem *et al.* (2005) and Ducrocq (2005) for Holstein cows in Canada and France, respectively.

6.4   Genetic correlations between longevity and fertility and production traits

Direct selection for longevity is a trait of great economic importance in beef and dairy cattle enterprises (Forabosco *et al.,* 2009; Banga *et al.,* 2013: 2014). But its inclusion in the breeding objective is hampered because the trait is lowly heritable (Kern *et al.,* 2014a; Van Pelt *et al.,* 2015) and the delay in availability of phenotypic information (Lagrota *et al.,* 2010; Melo *et al.,* 2014). Other challenges that hinder the selection for longevity include the proper measure of productive live compatible with short generation intervals and the choice of the right analysis that is capable of capturing environmental factors influencing the trait (Kern *et al.,* 2014a,b; Van Pelt *et al.,* 2015; Kern *et al.,* 2017). The challenge of selecting young bulls for longevity is compounded by the fact that majority of their daughters are still alive at the end of first lactation (Buenger *et al.,* 2001). The presence of large amounts of censored records leads to low accuracy of estimated breeding values for productive life (Vuksinovic *et al.,* 1999).   Accuracy of genetic evaluations for longevity can be increased by including information on other traits during analysis, preferably those expressed early in life (Larroque and Ducrocq, 2001; Buenger *et al.,* 2001). Such traits include type traits, which have been used to classify and identify desirable traits associations with longevity (Kern *et al.,* 2017).

Traits such as body size composite and udder traits have been reported to have significant influence on productive life in Lithuanian dairy cattle (Lavrinovic *et al.,* 2009). Kern *et al.* (2017) investigated the phenotypic correlation between longevity and type traits. However, this study did not find any significant association between type traits and risk of culling in Brazilian Holsteins. Contrary to this finding, other studies have reported udder traits especially udder depth and fore udder attachment to have a large impact on longevity (Sewalem *et al.,* 2005; Dadpasand *et al.,* 2008; Morek-Kopeć and Zernecki, 2012). Final score and angularity (dairy character) has also been found to significantly influence longevity in Czech Holsteins (Zavadilová *et al.,* 2011). Traits expressed early in life and which are favourably correlated with longevity can be used as selection criteria (Van Melis *et al.,* 2010). The current study systematically assessed the genetic associations between traits expressed early in life and longevity in the Sahiwal cattle in Kenya. In Chapter 4 of this study found that first lactation milk yield had the highest genetic correlation. Therefore this trait should be used as a selection criterion for longevity.

6.5 Inbreeding depression for traits of economic importance

Effects of inbreeding on the traits were determined by fitting four regression models (linear, quadratic, exponential and Michaelis-Menten) to the errors generated by the animal model. The linear, exponential and Michaelis-Menten models were significant ($P < 0.05$) for all the studied traits while the quadratic model was only significant ($P < 0.05$) for calving interval. Inbreeding had a positive effect on calving interval, age at first calving, and lactation length, shortening calving both interval and age at first calving and increasing lactation length. The relation between inbreeding and depression of traits was not linear, with greater depression after 15% inbreeding. Genetic evaluation of the Kenyan Sahiwal should account for inbreeding. However the results of the current study and those of Mahlado et al. (2013) indicate that as inbreeding level increases, inbreeding depression increases at an increasing rate. This could imply that at higher levels of inbreeding (>15%) apart from additive effects of inbreeding, there could be inter-locus interaction between loci with identical alleles by descent, leading increased depression.

The implications of these results have a profound effect on how inbreeding is accounted for in genetic evaluations. Most genetic evaluations either ignore inbreeding or fit a linear regression to account for inbreeding (Maiwashe et al., 2005; Mirhabibi et al., 2007; Mostert, 2011). The results of the current study indicate the need to consider effect of inbreeding on traits of economic importance, but not as a linear regression. The very high significance of the Michaelis-Menten model, which theoretically implies an increasing rate of depression as inbreeding level increases indicates that inbreeding should be accounted for using non-linear regression models. The mating plan for any breeding programme should be designed so as to control future rates of inbreeding while achieving genetic gain.

Closed nucleus breeding programmes, such as that for the Sahiwal cattle in Kenya are able to achieve faster rates of genetic gain but are associated with high inbreeding levels and low effective population sizes due to increased focus on a few high performing often closely related animals (Mwangi *et al.,* 2015). Although studies of inbreeding depression on longevity are rare, it has been shown that longevity, milk yield and reproductive performance decrease while, rate of disposal or loss of replacement heifers before first calving, age at puberty increase due to inbreeding through reduced growth (Du Toit *et al.,* 2012). For every increase of 1% in inbreeding, productive life has been reported to decrease by about 13 days

(CDN, 2008). Cows with high inbreeding level have also been reported to have a higher risk of being culled (Rokouei *et al.,* 2010), reduced reproductive efficiency and stayability.

6.6 Conclusions

i. Among measures of longevity survival from first calving to 96 months had the highest heritability estimate, and therefore should be used for genetic evaluation of longevity in Sahiwal cattle in Kenya.

ii. Inbreeding led to significant depression in fertility and production traits studied. The relationship between inbreeding and depression of traits was not linear, with greater depression after 15% inbreeding.

iii. First lactation milk yield had the highest genetic correlation with longevity, and should therefore be used as a selection criterion for longevity.

6.7. Recommendations

i. The genetic parameters estimated for longevity (heritability and genetic correlations) can be used to include the trait in the breeding objective of the Sahiwal cattle in Kenya

ii. Inbreeding should be routinely accounted for in genetic evaluation of the Sahiwal cattle breed by fitting non-linear models.

iii. Indirect selection for longevity can be achieved by selecting for first lactation milk yield to avoid lengthening generation interval and slowing rate of genetic gain due to direct selection for longevity.

iv. Further studies are required to compare response to direct and direct selection for longevity

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APPENDIX

A section of results from the 99999th and 100000th iteration and results from thrgibbs1f90 for long6

99999 rounds

 G

  37.99

 R

  1.100

    100000 rounds

 G

  36.24

 R

  1.088

elapsed time per iteration   2.5957188E-02 : total   2595.719

* End of iteration10-22-2019   18h 26m 56s 669

ave G

  43.67

SD G

  117.5

ave R

 0.9453

SD R

 0.1791

* Last seeds = 1347124817 1513694973

* Number of samples kept =   90000

solutions stored in binary file: "last_solutions"

****

***************** DIC *****************

****

detR 0.945296569542620

stored samples   90

D-bar   3821.96060348923

D(theta-bar)   14543.9597971043

DIC = 2*D-bar - D(theta-bar) = -6900.03859012582

Effective number of parameters = -10721.9991936150

solutions stored in file: "binary_final_solutions"

* End program10-22-2019 18h 26m 57s 131

C:\Users\USER\..blupf90>

C:\Users\USER\..blupf90>postgibbsf90

 name of parameter file?long6.par

long6.par

 POST-GIBBSF90 3.08

  # parameters in gibbs_samples =   2

 Read   90 samples from round   11000 to   100000

 Burn-in?

10000

 Give n to read every n-th sample? (1 means read all samples)

1000

Every n-th stored in gibbs_samples   1000

samples after burn-in =   80

samples after burn-in used =   80

******** Monte Carlo Error by Time Series ********

Pos.	eff1	eff2	trt1	trt2	MCE	Mean	HPD	Effective	Median	Mode
Independent										
							Interval (95%)	sample size		chain size
1	4	4	1	1	16.513	49.065	0.46650	275.30	55.4	5.7730
28.014			2							
2	0	0	1	1	0.24300E-01	0.93364	0.50310	1.2230	56.8	0.97680
1.0179			2							

******** Posterior Standard Deviation ********

Pos.	eff1	eff2	trt1	trt2	PSD	Mean	PSD	Geweke	Autocorrelations		
Independent											
							Interval (95%)	diagnostic	lag: 1	10	50 #
batches											
1	4	4	1	1	123.63	49.065	-193.25	291.38	-0.14	0.206	-0.051 -
0.038			40								
2	0	0	1	1	0.18424	0.93364	0.57254	1.2947	-0.06	0.136	-0.040
0.278			40								

Choose a graph for samples (= 1) or histogram (= 2); or exit (= 0)