A genetic evaluation of productive herd life in dairy cattle

by

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Table of contents

Declaration

I declare that the treatise hereby submitted by me for **Philosophiae Doctor** degree at the University of the Free State, is my own independent work and has not previously been submitted by me at any other University/Faculty. I furthermore cede copyright of the treatise in favour of the University of the Free State.

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Abstract

The length of productive life is of major economic importance in dairy cattle production. Simple breeding objectives such as selection for increased production in dairy cattle have led to a significant decline in fitness traits. A multi-purpose breeding objective that includes other traits such as length of productive life should be considered. Herd life reflects the ability of a cow to avoid being culled for low production, low fertility, or illness. Herd life can be used in breeding programs if genetic parameters are known. The objectives of the study were to: (1) estimate genetic parameters for functional herd life for the South African Jersey breed using a multiple trait linear model, (2) develop a prototype breeding value for functional herd life for the South African Jersey breed, (3) estimate genetic relationships between functional herd life and conformation traits in the South African Jersey breed and (4) assess inbreeding depression for functional herd life in the South African Jersey breed based on level and rate of inbreeding. A measure of herd life called functional herd life was considered in the current study. Functional herd life refers to herd life adjusted for milk production in the first lactation. In this study functional herd life was defined as survival in each of the first three lactations. Functional herd life was denoted by a 1 if a cow survived and 0 otherwise.

Analyses to estimate genetic parameters for functional herd life were carried out as follows. Data and pedigree records on purebred Jersey cows that participated in National Milk Recording and Improvement Scheme were analyzed. Data before editing comprised test-day and lactation yields on milk, fat and protein yields from 252 629 Jersey cows born between 1968 and 2005. After editing, 181 269 cow records from 636 herds recorded over 16 years were available for analysis. Estimates of genetic parameters for herd life were obtained using REML procedures fitting a multiple-trait linear animal and sire models. Heritability estimates (0.02 to 0.03) from the two models were somewhat similar for all lactations. However, heritability estimates for lactations 2 and 3 were slightly higher with the sire model compared to the animal model. The genetic correlation between lactations 1 and 2 from both the sire and animal models was higher than that between lactations 2 and 3. Genetic correlations from the sire model ranged from 0.68

to 0.99 and corresponding estimates from the animal model ranged from 0.76 to 0.99. Genetic parameters obtained in the current study suggest that sufficient genetic variation exist for herd life to allow for genetic improvement and that early selection for functional herd life is feasible.

The development of a prototype breeding value for functional herd life for the South African Jersey breed was carried out as follows. Test-day and lactation data on cows that participated in the National Dairy Cattle Improvement Scheme were considered. A multiple-trait linear animal model was used to estimate breeding values using Parameter ESTimation (PEST) software package. A complete (co)variance structure for the additive genetic and residual effects for the three traits were used. These (co)variances were estimated in the first objective. Reliabilities were approximated using the effective number of daughters. Estimated breeding values were scaled so that the average breeding value was a 100. Estimated breeding values for sires ranged from 79 to 114. The rate of genetic progress per year for the period 1985 to 2002 was statistically non-significant ($b = 0.02 \pm 0.05$ per year). The mean reliability was 33.43% and reflective of the low heritability of functional herd life. However, it should be noted that while direct selection for functional herd life could lead to genetic progress, this genetic response could be relatively slow due to the low heritability.

The genetic relationship between conformation traits and functional herd life of the South African Jersey population was investigated. Data on conformation traits (n = 46 238) and functional herd life (n = 90 530) on registered South African Jersey cows calving between 1989 and 2008 were obtained from the Integrated Registration and Genetic Information System. Conformation traits were scored using a subjective linear scoring system ranging from 1 to 9, except for foot angle with a maximum score of 8. Conformation traits included stature, chest width, body depth, dairy strength, rump angle, thurl width, rear leg side view, foot angle, fore udder attachment, rear udder height, rear udder width, udder support, udder depth, front teat placement, rear teat placement and front teat length. Genetic correlations between conformation traits and functional herd life were estimated using a series of bivariate analyses. The highest correlations were estimated for udder traits. Significant moderate to high positive genetic correlations between most udder traits and functional herd life (0.23 to 0.63) were estimated. The most important udder traits related to functional herd life were fore udder attachment, rear udder height, and udder depth. Correlations between the majority of body structure and functional herd life were variable. Most of the body structure traits had a low to moderate negative correlation with functional herd life (-0.04 to -0.27). The structural body traits of rump angle and foot angle were estimated to have a moderate positive genetic correlation with functional herd life. The genetic relationships between functional herd life and conformation traits in the South African Jersey breed indicate that conformation traits could be used to enhance the accuracy of genetic evaluation for functional herd life.

The effect of inbreeding depression on functional herd life in the South African Jersey population based on individual level and rate of inbreeding was investigated. A pedigree file of the South African Jersey breed (n = 912 638) was obtained from the Integrated Registration and Genetic Information System (INTERGIS). The data included registered, grade and imported animals. The percentages of animals in the pedigree file with two, one and zero parents unknown were 22%, 18% and 60%, respectively. The inbreeding coefficient for each animal (F_i) and the rate of individual inbreeding (ΔF_i), as an alternative measure of inbreeding which is adjusted for the depth of known pedigree, were calculated. The effect of inbreeding on functional herd life in each of the first three lactations was estimated using a single trait sire model on data collected from 1985 to 2003. Three analyses for survival in each of the first three lactations were conducted. In the first analysis, in addition to fixed and random effects, an individual inbreeding coefficient (F_i) was fitted as a linear covariate. In the second analysis, the inbreeding coefficient was included as a discrete variable with the following classes of inbreeding: $0 < F \leq 3.125$, $3.125 < F \leq 6.25$, $6.25 < F \leq 12.5$ and $F > 12.5$. In the third analysis, the individual rate of inbreeding (ΔF_i) was included in the model as a linear covariate. The level of inbreeding in the SA Jersey population showed a gradual increase for the period 1985 to 1994, while the period 1995 to 2009 showed a rapid increase. The current mean level of inbreeding (for the year 2010) is 4.85% with a minimum and maximum of 0 and 31.34%, respectively. The rate of inbreeding showed a gradual increase from 0.36% to 0.43% between 1985 and 2003. The average rate of inbreeding is currently (for the year 2010) at 0.55%. There was a significant ($P<0.05$) unfavourable relationship between inbreeding and functional herd life in the first and second lactation. The effect of inbreeding was more pronounced in the second lactation for both measures of inbreeding. Based on the current level of inbreeding, the reduction in functional herd life in the first lactation can be estimated to be 0.68%. The corresponding estimate for the second lactation is 1.70%. These results indicate that the current level or rate of inbreeding has reached levels that are detrimental to functional herd life. Therefore, individual inbreeding coefficient should be considered when breeding decisions are made by the Jersey breeders in addition to genetic merit.

Opsomming

Die produktiewe leeftyd van melkkoeie is van groot ekonomiese belang in melkbeesproduksiestelsels. Eenvoudige teeltdoelwitte, soos seleksie vir verhoogde produksie in melkbeeste, het tot ‘n betekenisvolle afname in fiksheidseienskappe gelei. ‘n Veeldoelige teeltdoelwit, wat ander eienskappe soos die lengte van produktiewe lewe insluit, behoort oorweeg te word. Kuddeleeftyd weerspieël die vermoë van koeie om nie weens lae melkproduksie, lae vrugbaarheid of siekte uitgeskot te word nie. Kuddeleeftyd kan, indien die genetiese parameters bekend is, in teeltprogramme gebruik word. Die doelwitte van die studie was om: (1) genetiese parameters vir funksionele kuddeleeftyd vir Suid-Afrikaanse Jerseys te beraam, deur van ‘n meervoudige-eienskap-liniêre model gebruik te maak, (2) ‘n prototipe teeltwaarde vir funksionele kuddeleeftyd vir Suid-Afrikaanse Jerseys te ontwikkel, (3) die genetiese verwantskappe tussen funksionele kuddeleeftyd en bouvormeienskappe vir Suid-Afrikaanse Jerseys te bepaal en (4) die afname in funksionele kuddeleeftyd in die Suid-Afrikaanse Jerseys populasie is gebaseer op die vlak- en tempo van inteling. In die huidige studie is kuddeleeftyd beskryf as funksionele kuddeleeftyd. Funksionele kuddeleeftyd verwys na kuddeleeftyd wat vir eerste laktasiemelkproduksie aangepas is. In hierdie studie is funksionele kuddeleeftyd gedefinieer as oorlewing gedurende elkeen van die eerste drie laktasies. Funksionele kuddeleeftyd is met ‘n 1 aangedui indien ‘n koei die laktasie oorleef het en met ‘n 0 (nul) indien nie.

Om die genetiese paramaters vir funksionele kuddeleeftyd te beraam, is die beramings as volg uitgevoer: Die melkproduksie- en stamboomrekords van suiwergeteelde Jerseykoeie wat aan die Nasionale Melkaantekening en Verbeteringskema deelgeneem het, is in die analise gebruik. Voor die redigering van die data, het dit bestaan uit die toetsdag- en laktasierekords vir melk-, vet- en proteïenproduksie van 252 629 Jersey koeie wat tussen 1968 en 2005 gebore is. Na die redigering was produksierekords van 181 269 Jerseykoeie in 636 kuddes oor ‘n 16-jaar tydperk vir ontleding beskikbaar. Beramings van genetiese parameters vir kuddeleeftyd is verkry deur middel van REML-prosedures deur die passing van meervoudige-eienskap liniêre diere- en

vaarmodelle. Oorerflikheidswaardes soos beraam deur beide modelle, was grootliks dieselfde vir alle laktasies, naamlik 0.02 tot 0.03. Die oorerfliksheidsberamings vir laktasie 2 en 3 was egter ietwat hoër vir die vaarmodel in vergelyking met die dieremodel. Die genetiese korrelasie tussen laktasies 1 en 2 vir beide die vaar- en dieremodel was hoër as diè tussen laktasies 2 en 3. Die genetiese korrelasies van die vaarmodel het vanaf 0.68 tot 0.99 gevarieer en die ooreenstemende beramings van die dieremodel het gewissel vanaf 0.76 tot 0.99. Die genetiese parameters wat in dié studie verkry is, dui daarop dat voldoende genetiese variasie ten opsigte van kuddeleeftyd bestaan om genetiese vordering te behaal en dat vroeë seleksie van funksionele kuddeleeftyd haalbaar is.

Die ontwikkeling van ‘n prototipe teeltwaarde vir funksionele kuddeleeftyd vir Suid-Afrikaanse Jerseys is as volg uitgevoer: Toetsdag- en laktasierekords van koeie wat aan die Nasionale Melkaantekening en Verbeteringskema deelgeneem het, is vir die ontleding gebruik. ‘n Meervoudige-eienskap-liniêre dieremodel is gebruik om teeltwaardes met behulp van die Parameter ESTimation (PEST) sagtewarepakket te beraam. ‘n Volledige (ko)variansie struktuur is vir die additiewe genetiese- en residuele-effekte vir die drie eienskappe gebruik. Dié (ko)variansies is in die eerste doelwit beraam. Betroubaarhede is gekorrigeer deur die effektiewe getal dogters te gebruik. Beraamde teeltwaardes is gerangskik met 100 as die gemiddelde teeltwaarde. Beraamde teeltwaardes van bulle het tussen 79 en 114 gewissel. Die tempo van die jaarlikse genetiese vordering, vir die periode 1985 tot 2002, was statisties nie-betekenisvol (b = 0.02±0.05 per jaar). Die gemiddelde betroubaarheid was 33.43% en weerspieël die lae oorerflikheid van funksionele kuddeleeftyd. Dit moet egter in gedagte gehou word dat, hoewel direkte seleksie vir funksionele kuddeleeftyd tot genetiese vordering mag lei, die genetiese vordering relatief stadig sal wees weens die lae oorerflikheid van die eienskap.

Die genetiese verband tussen bouvormeienskappe en funksionele kuddeleeftyd is vir die Suid-Afrikaanse Jersey populasie bepaal. Data oor die bouvormeienskappe (n = 46 238) en funksionele kuddeleeftyd (n = 90 530) van geregistreerde Suid-Afrikaanse Jerseykoeie wat tussen 1989 en 2008 gekalf het, is vanaf die Integreerde Registrasie en Genetiese Informasie Stelsel (INTERGIS) verkry. Bouvormeienskappe is gepunt volgens ‘n subjektiewe liniêre punteskaal wat tussen 1 en 9 varieer met die uitsondering van hoefhelling wat ‘n maksimum punt van 8 het. Die volgende bouvormeienskappe is ingesluit: skofhoogte, borsbreedte, liggaamsdiepte, suiwelsterkte, kruishelling, kruisbreedte, agterbeen syaansig, hoefhelling, vooruieraanhegting, agteruierhoogte, agteruierbreedte, mediale ligament, uierdiepte, voorspeenplasing, agterspeenplasing en voorspeenlengte. Genetiese korrelasies tussen bouvormeienskappe en funksionele kuddeleeftyd is deur ‘n reeks twee-eienskap ontledings bepaal. Die hoogste korrelasies is tussen funksionele kuddeleeftyd en uiereinskappe verkry. Die positiewe en betekenisvolle genetiese korrelasies tussen die meeste uiereinskappe en funksionele kuddeleeftyd was matig tot hoog. (0.23 tot 0.63). Die belangrikste uiereienskappe wat met funksionele kuddeleeftyd verband gehou het, was vooruieraanhegting, ageruierhoogte en uierdiepte. Die korrelasies tussen die meeste eienskappe ten opsigte van liggaamstruktuur en funksionele kuddeleeftyd was varierend. Die meeste eienskappe het ‘n lae tot matige negatiewe korrelasie met funksionele kuddeleeftyd getoon (-0.04 tot -0.27). Die ontleding het getoon dat strukturele bouvormeienskappe soos kruishelling en hoefhelling ‘n matige positiewe genetiese korrelasie met funksionele kuddeleeftyd het. Die genetiese verband tussen funksionele kuddeleeftyd en bouvormeienskappe vir Suid-Afrikaanse Jerseys dui daarop dat bouvormeienskappe gebruik kan word om die akkuraatheid van genetiese evaluasies van funksionele kuddeleeftyd te verhoog.

Die effek van die vlak- en tempo van inteling op die afname in funksionele kuddeleeftyd is vir Suid-Afrikaanse Jerseys beraam. ‘n Stamboom lêer van die Suid-Afrikaanse Jerseyras (n = 912 638) is vanaf INTERGIS verkry. Die datalêer het geregistreerde, graad en ingevoerde diere ingesluit. Die aantal diere in die stamboomlêer met twee, een en geen onbekende ouers nie, was 22%, 18% en 60%, onderskeidelik. Die inteeltkoëffisient van elke dier (F_i) en die tempo van indiwiduele inteling (ΔF_i), as ’n alternatiewe inteeltmaatstaf, aangepas volgens bekende stamboominligting, is beraam. Die effek van inteling op funksionele kuddeleeftyd in elkeen van die eerste drie laktasies is bereken deur ‘n enkel-eienskap vaarmodel toe te pas op data wat tussen 1985 en 2003 ingesamel is. Drie ontledings vir oorlewing is uitgevoer in elkeen van die eerste drie laktasies. In die eerste ontleding, benewens vaste en ewekansige effekte, is ‘n indiwiduele inteeltkoëffisient (F_i) as ‘n liniêre ko-variansie gepas. In die tweede ontleding is die inteeltkoëffisient as ‘n diskrete veranderlike ingesluit, met die volgende klasse van inteling:

$0 < F \leq 3.125$, $3.125 < F \leq 6.25$, $6.25 < F \leq 12.5$ en $F > 12.5$. In die derde ontleding is die indiwiduele tempo van inteling (ΔF_i) in die model as ‘n liniêre ko-variansie ingesluit. Die vlak van inteling in die Suid-Afrikaanse Jersey populasie het vanaf 1985 tot 1994 ‘n geleidelike toename getoon, terwyl ‘n vinniger toename vanaf 1995 tot 2009 waargeneem is. Die huidige (vir 2010) gemiddelde vlak van inteling is 4.85% met ‘n minimum en maksimum waarde van 0 en 31.34% onderskeidelik. Die tempo van inteling het ‘n geleidelike toename vanaf 0.36% tot 0.43% tussen 1985 en 2003 getoon. Die huidige gemiddelde tempo van inteling (vir 2010) is 0.55%. Daar was ‘n betekenisvolle ongunstige verband tussen inteling en funksionele kuddeleeftyd vir eerste en tweede laktasie. Die effek van inteling was meer waarneembaar in die tweede laktasie vir beide inteeltmaatstawwe. Gebaseer op die huidige vlak van inteling, kan die vermindering in funksionele kuddeleeftyd vir eerste laktasie, as 0.68% bereken word. Die ooreenstemende beraming vir tweede laktasie is 1.70%. Hierdie resultate toon dat die huidige vlak of tempo van inteling vlakke bereik het wat nadelig is vir funksionele kuddeleeftyd. Die indiwiduele inteeltkoëffisient moet dus tesame met genetiese meriete, deur Jersey telers in ag geneem word wanneer teeltbesluite geneem word.

Chapter 1

General introduction

Yield traits of dairy cows are recorded routinely in many countries and breeding values for these traits are easily obtained. Milk yield and its components are the most important traits in dairy cattle production, and genetic progress of these traits is well documented. However, high milk yields may be associated with physical or physiological changes that tend to limit further increases in productive or economic herd life; for instance, high yielding cows are more susceptible to mastitis, milk fever and ketosis (Jairath *et al*., 1994). A major focus of dairy producers should be on improving productive life and therefore maximizing the profitability of the cow. An increased herd life is associated with reduced replacement costs and increased possibility for selection on other traits (Vukasinovic *et al*., 2002). Long productive life allows exploitation of optimum milk capacity of the cow and increased voluntary culling (Cruickshank *et al*., 2002).

Herd life of dairy cow measures the time she produces in the herd, and it is determined by her milk production, health, fertility and workability. Traits reflecting the production of a cow are usually called primary traits, and traits reflecting health, fertility, and workability, secondary traits. In the literature, various definitions for herd life are used. A distinction can be made between (functional) ‘corrected” and (productive) “uncorrected” herd life. Corrected herd life is adjusted for milk production, thus aiming to give better measurements of involuntary culling (Cruickshank *et al*., 2002). Corrected herd life is also called functional, similar to traits causing involuntary culling such as diseases, which are also called “functional” traits. Roxström & Strandberg (2002) stated that reasons for culling can range from reproductive and health problems to severe injury and accidents. Therefore, they have defined functional herd life into smaller components, namely, fertility-, mastitis- and production-determined length of productive life. Hereafter, functional and productive herd life will be used interchangeably.

Management decisions made by dairy farmers and natural death of cows are the main determinants of actual herd life of cows. There should be a clear distinction between culling reasons for production and culling for functional traits. To make an accurate assessment for culling reasons, it is therefore important that farmers should be encouraged to record the correct culling reasons at all time. This information could be useful in improving functional herd life. There are four ways by which herd life could increase profit (Rendel & Robertson, 1950):

1. by reducing the annual costs of replacements per cow in the herd,
2. by increasing the average herd yield through an increase in the proportion of cows in the higher producing age-groups,
3. by reducing the replacements that have to be reared, and therefore allowing an increase in size of the milking herd and
4. by an increase in the possibilities for voluntary culling.

The actual profit from an increased herd life of cows depends on the production circumstances of the farmer. Several authors concluded that the proportion of involuntary culling governs the economic advantage of herd life (Van Arendonk, 1985; Dekkers, 1993; Stott, 1994). The economic value of herd life has often been estimated. In their review, Van Raden & Wiggans (1995) concluded that the ratio between the relative economic values for yield and herd life was on average 2.5:1 with a range of 0.8:1 to 8.0:1. The wider range emphasize that the economic value of herd life depends on the production circumstances, although some variation is also caused by the difference in methods used to calculate the economic value.

In 1970 the average length of productive life in the South African Jersey population was 7.9 lactations, followed by a gradual decline to 4.1 lactations in 1977, to reach an average length of productive life of 2.3 lactations in 1994 (Du Toit *et al*., 2004). The reasons for this decline in herd life can be the restructuring of pricing systems applied by the major milk buyers, carcass price of culled cows, and the tendency to concentrate on maximum production for milk in the mid-eighties. Nowadays much emphasis is on sustainability of production systems and welfare of animals and in this respect an increased herd life would be one of the desired changes in dairy production. By including herd life into breeding programs, organizations can contribute at least to the increase of potential herd life of dairy cows. Availability of breeding values for herd life would allow dairy farmers to improve the overall sustainability of their enterprises.

As already indicated there are many ways to define herd life. Therefore, identifying a measure of herd life applicable for the population of interest is important. It is important to note that data available can limit the choice of a measure of herd life. Herd life of cows can be easily calculated from milk recording records, if one assumes that the last known test day is the last day of a cow's life. Because herd life is determined by production and functional traits, herd life corrected for milk production (functional herd life) is a better measure than uncorrected herd life (Dekkers, 1993). Van Arendonk (1985) showed that culling decisions are always taken on a within herd basis, which indicates that correction for production should be on a within herd basis. In many studies, this correction has been done using the production in the first lactation compared with that of herd mates (Rogers *et al*., 1991b; Short & Lawlor, 1992; Vollema & Groen, 1996). In contrast, Boldman *et al*. (1992) used production in the last lactation. References that used production in first lactation argued that production in last lactation may be influenced and be reduced due to factors like illness. Using production in the last lactation, would then overestimate the functional herd life. Assuming that the repeatability of production over lactations equals one, it would be best to use production in the first lactation (Vollema & Groen, 1998).

In general, heritability estimates of herd life are low. Caraviello *et al*. (2004) reported heritability estimates for herd life ranging from 0.05 to 0.13. Similarly, Smith & Quaas (1984) found heritablilty estimates of 0.06 and 0.13 from two data sets that were derived from different data selection strategies. Vollema & Groen (1998) reported heritability estimates ranging from 0.02 to 0.08. Buenger *et al*. (2001) and Sewalem *et al*. (2005) using a Weibull model, reported heritability estimates for functional length of productive life that were much higher (0.09 to 0.14) than estimates obtained with other methodologies. They reinforced the idea of moving from linear models towards survival (Weibull) models to analyze herd life traits in dairy cattle. The low heritability estimate for total lifetime performance traits suggest that direct selection for lifetime performance traits holds little promise for enhancing lifetime performance of cows, because response to selection is slow (Jairath *et al*., 1994).

An alternative that can be used to predict herd life is an indirect prediction of herd life from conformation traits (Larroque & Docrocq, 2001). Schneider *et al*. (2003) reported that the traits describing the udder, feet and legs and hooves strongly influenced ability of animals to stay in the herd. Similarly, Sewalem *et al*. (2004) confirmed that the length of herd life was particularly associated with udder, foot and leg and hoof traits. Even though indirect predictions of genetic values are often available earlier than direct predictions in an animal's life, their usefulness for selection also depends on their relative reliability. Although the reliability of direct prediction will eventually approach unity with many effective progeny, the low heritability of functional herd life results in the need for many effective progeny to attain high reliability values. As a result of the moderate estimated heritabilities of linear traits, however, when the effective progeny is less than 75, indirect prediction from linear traits is more accurate than direct prediction (Boldman *et al*., 1992). This is in agreement with results from Brotherstone *et al*. (1998) who showed the diminishing effect of type data as the number of progeny with lifespan observations increased. Udder traits should receive the most emphasis of all type traits. This is in agreement with results from Dekkers *et al*. (1994) and Liu *et al*. (2004), reporting that the strongest relationships for herd life traits were associated with udder conformation and feet and legs in registered cows.

It is evident that improved conformation traits can positively influence the functional herd life of cows and thus the economic efficiency of the herd. Besides being measured early in life, conformation traits are more heritable than herd life (Caraviello *et al*., 2003). Genetic evaluation for herd life including correlated conformation traits may be more accurate than evaluations based on survival information alone (Boldman *et al*., 1992).

The aim of this study was to develop the framework for the implementation of a national genetic evaluation system for herd life in the South African Jersey breed. This aim was achieved using the following specific objectives:

1. To estimate genetic parameters for functional herd life for the South African Jersey breed using a multiple trait linear model
2. To develop a prototype breeding value for functional herd life for the South African Jersey breed

3. To estimate genetic relationships between functional herd life and conformation traits in the South African Jersey breed
4. To assess inbreeding depression for functional herd life in the South African Jersey breed based on level and rate of inbreeding

The thesis is structured as follows:

After a general introduction in Chapter 1, an overview of the literature containing estimates of heritabilities of herd life, genetic and phenotypic correlations between herd life and conformation traits, are presented in Chapter 2. In Chapter 3 the genetic parameter estimates for functional herd life for the South African Jersey breed, using multiple trait sire and animal linear models, are presented. In Chapter 4 the framework for implementation of a national genetic evaluation for functional herd life has been developed. In Chapter 5 the relationships between functional herd life and conformation traits are presented. Results of inbreeding depression for functional herd life based on level and rate of inbreeding are presented in Chapter 6. In the general discussion (Chapter 7), issues concerning the incorporation of herd life in the national genetic analysis of the South African Jersey breed that were addressed in the previous chapters, are summarized and related to the South African situation.

Chapter 2

Literature review on herd life in dairy cattle

2.1 Introduction

Herd life is one of the most important breeding objective traits in dairy cattle production. Therefore, it has received tremendous attention in most national genetic programmes for dairy cattle. Functional herd life is a product of production and the ability to sustain involuntary culling. However, high milk yields may be associated with physical or physiological changes that tend to limit further increases in productive or economic herd life; for instance, high yielding cows are more susceptible to mastitis, milk fever and ketosis (Jairath *et al*., 1994). To maximize the profitability of the cow, dairy farmers should be more concerned in extending the productive life of the cow, even if the approach leads to sub-optimal genetic progress in milk production and component traits (Jairath *et al*., 1994). Long productive life allows exploitation of maximum milk capacity of the cow and increased voluntary culling. Genetic improvement for longevity through direct selection has been hampered by its low heritability estimate. Conformation traits are generally used to enhance the accuracy of genetic evaluation for longevity since they are moderate to highly correlated with herd life. In addition, conformation traits are expressed early in life.

Extensive research has been conducted on herd life focusing mainly on identifying measures of herd life that are expressed early in life, estimating heritabilities and genetic correlations between herd life and conformation traits and development of a comprehensive genetic evaluation system for herd life. In addition, research has also focused on evaluation of different models for genetic analysis of herd life in search of a more practical model. This literature review focuses on: measures of herd life, methods used to analyse herd life data and genetic parameters for herd life and conformation traits. The summary section at the end of this chapter highlights part of the literature review that is relevant to the research conducted in this study.

2.2 Measurements of herd life

Various definitions for herd life or longevity are used in the literature. A distinction can be made between ‘corrected” and “uncorrected” herd life. Corrected herd life is corrected for milk production, thus aiming to give better measurements of involuntary culling (Dekkers, 1993). Corrected traits are also called “functional” herd life, similar to traits causing involuntary culling such as diseases, which are called “functional” traits. Terms commonly used to categorize longevity are “lifetime” or “stayability”. Lifetime traits do contain all available information during the lifespan of a cow, but can be measured only after the death of the cow. Stayability traits measure whether or not a cow is alive at a certain point in time (e.g., at a fixed number of months from birth to first calving). Although stayability traits can be measured at any time, they contain less information than traits that measure the entire lifespan of a cow. For instance, a cow that did not survive up to 36 months of age can have any lifespan that is shorter than those 36 months, and if she did survive, it is unknown how much longer she will live. Stayability to a fixed age is not an ideal measure of herd life, because of the binomial nature of the data and because of the limited number of records available (Famula, 1981). A continuous measure of herd life would be preferable, but waiting that all cows have completed their herd life is not feasible. As stated by Vollema (1998), a compromise between the higher information content of lifetime traits and the earlier availability of stayability traits is to use opportunity groups. Opportunity groups consist of animals with the same maximum lifespan that can be recorded. Instead of waiting until all have been culled, a maximum lifespan (opportunity) is assigned to cows. If they are culled before this maximum is reached, their actual lifespan is known, otherwise the maximum opportunity is taken as their lifespan.

Vollema (1998) divided longevity or herd life traits into four classes, namely, lifetime, stayability, miscellaneous, and functional traits. The following definitions and abbreviations, as referred to in the tables, were given:

Lifetime traits:

- Herd life : time period between birth and culling
- length of productive life : time period between first calving and culling
- total milk production : lifetime milk production summed over lactations

- number of days in lactation : lifetime milking days summed over lactations
- number of lactations

Stayability traits:

- stayability until a certain number of months of age
- stayability until a certain number of months after first calving
- survival of a certain lactation

Miscellaneous trait:

- total months in milk at 84 months of age
- probability of surviving from one lactation to the other

Functional traits:

- herd life traits corrected for production are indicated by a prefix “functional”

2.3 Methods used to analyze herd life data

Different statistical models have been used for genetic analysis of herd life data. These different models are underpinned by different assumptions and therefore have different advantages regarding simplicity of implementation and requirements for computing resources. These models include survival analysis, linear and threshold models. Survival analysis and linear models have been used extensively while the threshold model has rarely been used due to computational difficulties. This is despite the fact that the threshold model is statistically more appropriate for binary survival traits than the linear model (Boettcher *et al*., 1999a). Therefore, survival analysis and linear model are reviewed here. Each of the two most important approaches normally used for the analysis of herd life had some advantages as well as disadvantages.

According to Forabosco *et al*. (2006) the linear model is:

1. Simple to implement and requires less computing resources.
2. Capable of implementing multiple-trait models where as only single trait models can be fitted in survival analysis.

3. Not able to readily include information on cows that survived at least three parities. The only way to include this variability in survival at an advanced age is to analyze the parities up to the last one observed in the data.
4. Not able to give an estimation of survival for each day during the entire productive life but only at some specific moments.
5. Not able to accurately account for the management and environmental effects, herd-year, variation in herd size and stage of lactation, which are time dependent variables that affect the cow's herd life.

Survival analysis is increasingly being used for analysis of herd life in animal breeding (Dürr *et al*., 1999; Buenger *et al*., 2001; Lubbers *et al*., 2000; Strandberg & Roxström, 2000). Survival analysis combines information on uncensored and censored individuals and therefore enables a proper statistical treatment of censored records and accounts for nonlinear characteristics of longevity data (Vukasinovic *et al*., 2001). Survival analysis generally provides better fit to the survival data because of the ability to properly account for the skewed distribution of survival data. On a lactation basis it also leads to a simpler data handling, reduced number of elementary records and reduced computational time compared with a survival analysis across lactations (Ducrocq, 1999).

Survival analysis offers several advantages over the linear model:

1. Time-dependent variables can be used for survival analysis to model accurately the effects of management and environmental factors such as contemporary group and stage of lactation (Boettcher *et al*., 1999a; Sewalem & Kistemaker, 2003; Caraviello *et al*., 2004).
2. Precision can be increased by accounting for differences in days of productive life between cows that survive for the same number of lactations (Veerkamp *et al*., 2001; Sewalem & Kistemaker, 2003).
3. Survival analysis includes censored records allowing the use of partial lactations of surviving cows to add information to the analysis (Boettcher *et al*., 1999a; Sewalem & Kistemaker, 2003; Caraviello *et al*., 2004), but its reliability mainly depends on the proportion of uncensored records (Vukasinovic *et al*., 1997; Vollema *et al*., 2000).

4. Survival analysis also tends to give greater estimates of heritability than does the linear model suggesting increased reliability of sires EBV and increased selection accuracy (Sewalem & Kistemaker, 2003).
5. Survival analysis allows use of non-linear models (Vollema & Groen, 1998).

Despite the relatively large amount of computer capacity that is needed to perform the analysis, several countries are currently using survival analysis for genetic evaluation of sires for survival of their daughters (e.g. France, Germany, the Netherlands, Denmark and Italy). This has been facilitated by the development and implementation of survival analysis in the Survival Kit software (Ducrocq & Sölkner, 1998).

2.4 Genetic parameters

Many researchers have estimated genetic parameters for longevity traits and the results are given in several tables and will be discussed as such. In each table the author(s), estimates of either heritability or correlation, number of records used in the analysis, model and method of the analysis, and applicable remarks are given. Summarized data are on Holstein cows, unless the breed is stipulated under remarks.

2.4.1 Heritability estimates

Five traits were used to define herd life, namely, herd life (HL), length of productive life (LPL), total milk production (TMP), number of days in lactation (NDL), and number of lactations (NLC). Table 2.1 presents heritability estimates of uncorrected lifetime traits.

For herd life, most estimates are in the range of 0.03 to 0.13. In the analysis of herd life Boldman *et al*. (1992) used a subset of those data used in the type analysis. Twenty one percent of the cows were still in the herd at 72 months and were assigned a herd life value of 2 190 days. This value underestimates the actual herd life because longer herd lives were possible for those 21% cows. Using REML in the analysis, a heritability estimate for herd life was 0.03.

Dentine *et al*. (1987) reported an average herd life of 1 821 days in grade Holstein cows in an analysis with an upper limit of six calvings and also reported a heritability estimate of 0.03

using Henderson's method 3. The low heritability for total lifetime performance traits suggest that direct selection for lifetime performance traits holds little promise for enhancing lifetime performance of cows (Jairath *et al*., 1994). Another practical problem is the large number of daughters (100 to 200 daughters per sire) needed to attain reasonable reliability of genetic evaluations for traits with such low estimated heritabilities.

Caraviello *et al*. (2004) reported heritability estimates for herd life ranging from 0.05 in the West to 0.13 in the West North Central region of the United States. The results may reflect differences in the magnitude of genetic variation in cow longevity between regions, although they could result from differences in accuracy of sire identification or record keeping between regions.

Zavadilová *et al*. (2009) in a study on Czeck Fleckvieh cows, reported a heritability estimate of 0.05 for functional length of productive life. A much higher heritability estimate (0.20) for functional longevity was reported by Vukasinovic *et al*. (2002) in Simmental cattle.

Vollema & Groen (1996) using a sire model, estimated heritability for herd life for different data sets on cows born in 1978, 1982 and 1985. The estimates decreased (0.14 to 0.04) with increasing year of birth. Heritability estimates were comparable with literature values, but differences between year of birth were quite large. The authors claimed that a) the population has been under strong selection during the period considered, (b) the percentage of Holstein genes increased tremendously, and (c) under the quota system, dairy producers base culling decisions on shorter term, thus increasing environmental variation of herd life traits. Analyzing the same data with both a sire and animal model gave similar results (0.04 and 0.037). When longevity traits with low heritability estimates (such as herd life) are analyzed with an animal model, most information also comes from the sire component. The difference between sire and animal models is therefore expected to be small (Vollema & Groen, 1996).

Using survival analysis, Buenger *et al*. (2001) reported a heritability estimate on the log scale of 0.116 and 0.111 for uncorrected length of productive life and functional length of productive life, respectively. This was consistent with results from survival analysis given by Dürr *et al*. (1999) of 0.09 and Hoque and Hodges (1980) of 0.10 using Henderson's method 3. Vollema & Groen (1996) using REML, reported estimates of heritability for length of productive life of 0.14 and 0.11 for Holstein cows born in 1978 and 1982, respectively. The higher heritability estimates were reported for uncorrected herd life (0.17) and functional herd life (0.18) when transformed to the original scale (Buenger *et al*., 2001). The transformation method of Yazdi *et al*. (2002) was used, which is independent of the value of the Weibull parameter used.

Rogers *et al*. (1991a) used data on grade and registered Jersey cows, while Short & Lawlor (1992) used data on grade and registered Holstein cows. The heritability estimates for length of productive life were consistently lower for the Jersey cows. Both authors reported the highest heritability estimates for registered cows with intermediate values for the combined data. Using Henderson's method 3, Hoque & Hodges (1980) estimated a low heritability for total lifetime milk of 0.11. This is in agreement with results reported by Jairath *et al*. (1994) of 0.13.

Heritability estimates for total milk production given by Vollema & Groen (1996) ranged from 0.09 to 0.17. The lower estimate from the animal model compared to the sire model was unexpected. Animal models account for the effect of prior selection, which might have been greater for milk production.

Jairath *et al*. (1994) reported relatively low heritability estimates for length of productive life and number of lactations in the range from 0.07 to 0.09. This is in agreement with results from Brotherstone *et al*. (1997), Hoque & Hodges (1980) and Van Raden & Klaaskate (1993). Vollema & Groen (1996) found heritability estimates for number of days in lactation and number of lactations for cows born in 1978 that were generally higher than those reported in Table 2.1. Estimates decreased with increase in year of birth.

Table 2.1 Literature heritability estimates (± SE), number of records, statistical models and methods used and remarks of analyses of uncorrected lifetime traits

	Estimates								
Author	**HL**	**LPL**	**TMP**	**NDL**	**NLC**	**Records**	**Model**	**Method**	**Remarks**
Hoque & Hodges (1980)	0.10 ±.02	0.10±.01	0.11±.02		0.09±.01	30 738	SM	Henderson III	Holstein cows
Smith & Quaas (1984)	0.13					227 091	Cox SM	Survival analysis	datasets dependent on definition of censored records Holstein cows
	0.06					449 325			
Dentine *et al.* (1987)	0.03					7 924	SM	Henderson III	Holstein grade cows
	0.03					15 868			registered cows
	0.04±.002					23792			combined data
Rogers *et al.* (1991a)		0.02				> 119 000	SM	REML	Jersey, grade cows
		0.04							Jersey, registered cows
		0.03							Jersey, combined cows
Boldman *et al.* (1992)	0.03					53 830	SM	REML	Holstein grade cows
Short & Lawlor (1992)	0.04[1]					45 515	SM	REML	Holstein grade cows
	0.10[1]					80 126			registered cows
	0.07[1]					125 887			combined data
Van Raden & Klaaskate (1993)					0.09	1 984 038	SM	REML	
Jairath *et al.* (1994)		0.08[2]	0.13[2]	0.09[2]	0.07[2]	82 835	SM	REML	Holstein cows
Vollema & Groen (1996) [3]	0.14	0.14	0.17	0.14	0.13	94 935	SM	REML	Holstein cows born in 1978
	0.11	0.11	0.13	0.12	0.12	166 324	SM		Holstein cows born in 1982
	0.04	0.04	0.10	0.05	0.03	38 957	SM		Holstein cows born in 1985
	0.04	0.04	0.09	0.04	0.04	38 957	AM		Holstein cows born in 1985

Brotherstone *et al.* (1997)					0.06	25 227	SM	REML	registered HF cows
Vollema & Groen	0.13				0.11	11 558	SM	REML VCE	Holstein cows born in 1978
(1997)	0.10				0.09	39 252			Holstein cows born in 1982
Dürr *et al.* (1999)		0.09				331 147	Weibull	Survival analysis	Holstein cows logarithmic scale
Buenger *et al.*		0.12				169 733	Weibull	Survival analysis	logarithmic scale
(2001)		0.17				169 733	Weibull		original scale
Tsuruta *et al.* (2005)	0.09	0.09				392 800	SM	Gibbs sampling	Holstein 305-day limited milk
Zavadilová *et al.* (2009)		0.05				58 493	AM	REML VCE	Czech Fleckvieh calved from 1994 to 2003

HL = herd life; LPL = length of productive life; TMP = total milk production; NDL = number of days in lactation; NLC = number of lactations; SM = sire model; AM = Animal model

[1] Approximate standard errors were ≤ .01

[2] SE ≤ .02

[3] Standard error of estimates ranged from .003 to .01

Tsuruta *et al*. (2005) reported heritability estimates of 0.10 for productive life when milk production was restricted to 305 days per lactation, and 0.09 for herd life. However, differences between these estimates were not significant.

Because lifetime traits can only be measured after a longer period of time, their superiority in breeding programs might be limited because of the prolonged generation interval. Another alternative might be the use of survival analysis because this method allows for incomplete lifetime records (Vollema & Groen, 1996). Heritability estimates of total milk production are generally higher than those of other lifetime traits, as can be expected, because total milk production is a product of length of productive life and the highly heritable milk production per day (Vollema & Groen, 1998).

In a REML analysis using a sire model, dams are assumed to be unrelated and heritability estimates may therefore be biased upwards. To check the magnitude of this bias, Brotherstone *et al*. (1997) performed a number of bivariate animal model analyses. The estimates from the animal model were similar to those from the sire model and suggested that the bias in the results from the latter is small.

Madgwick & Goddard (1989) split their data set into two subsets: cows first calving before 1979 and cows first calving after 1979. The heritability estimates of all the survival scores were low, ranging from 0.004 to 0.053. Survival post first calving had a higher heritability than subsequent lactations, as well as for cows calving before 1979 compared to cows calving after 1979. The reason for the differential survival between the breeds may be due to the change in breed structure from predominantly Jersey to Holstein Friesian cows.

Visscher & Goddard (1995) found higher heritability estimates for Jersey cows compared to Holstein cows. For both breeds, separate data were extracted: one for cows that had the opportunity to start a second lactation and another for cows that had the opportunity to stay until lactation 6. For the first data set the primary interest was in the parameters for first lactation yield and their correlation with early survival (lactation1 to 2). The second data set was analyzed to obtain correlations between several stayabilities and their correlation with first lactation milk records. Heritability estimates were consistently higher for the stayability of a certain lactation compared to the survival of a certain lactation given survival of the previous lactation.

Heritability estimates, number of records, statistical models and methods used and remarks of survival of a certain lactation (i= lactation number) from literature are presented in Table 2.2.

Both Rogers *et al*. (1991b), on Jersey cows, and Short & Lawlor (1992), on Holstein cows, conducted analyses using registered data and grade data separately, as well as combined registered and grade data. Rogers *et al*. (1991b) reported higher estimates of heritability for survival to the second lactation than Short & Lawlor (1992), most probably due to the correction to an underlying normal scale. Both authors reported the highest heritability for registered cows.

In an analysis of survival in the first three lactations, Boettcher *et al*. (1999a) made use of three methods. Using a linear model, heritability estimates for all three lactations were approximately 0.04, which was rather low and within the range of previously published estimates (Boldman *et al*., 1992; Madgwick & Goddard, 1989; Jairath *et al*., 1998) of heritability estimates for herd life traits estimated with linear models.

As expected, estimates of the parameters from the threshold model were higher than those from the linear model. Heritability estimates on the underlying scale were approximately 0.07 for all lactations and were not significantly different. Compared with results from the linear and threshold models, the heritability estimates were higher using survival analysis (0.09 and 0.12 for lactations restricted to 305 days and unrestricted 305 days, respectively). Perhaps the modeling of herd x year effects as time-dependent covariates provided a better fit and thus accounted for a greater proportion of the variance (Boettcher *et al*., 1999a).

Literature heritability estimates, number of records, statistical models and methods used, corrections made and remarks of analyses of functional lifetime traits are presented in Table 2.3.

As with uncorrected lifetime traits, five traits were used to define functional longevity; number of lactations initiated, total milk production regardless of lactation length, days in lactation over all lactations, time between birth and last test day (herd life), time between first calving and last test day (length of productive life).

Table 2.2 Literature heritability estimates (± SE), number of records, statistical models and methods used and remarks of survival of a certain lactation (i= lactation number)

	Estimate for lactation i									
Author	**i = 1**	**i = 2**	**i = 3**	**i = 4**	**i = 5**	**i = 6**	**Records**	**Model**	**Method**	**Remarks**
Madgwick & Goddard (1989)[1]	0.05±.02	0.01±.01	0.01±.01	0.02±.01	0.04±.02	0.02±.01	253 000	SM	REML	1 st calving < 1979
	0.03±.01	0.01±.01	0.01±.01	0.01±.01	0.01±.01					1 st calving > 1979
Brotherstone & Hill (1991a)		0.05	0.07	0.07			19 294	SM	REML	classified Holstein herds
Rogers *et al.* (1991a)[2]	0.05						22 179	SM	REML	Jersey, grade cows
	0.08						97 316			Jersey, registered cows
	0.08						119 817			Jersey, combined data
Short & Lawlor (1992)	0.01[3]						45 515	SM	REML	Holstein grade cows
	0.03[3]						80 126			Holstein registered cows
	0.02[3]						125 887			Holstein combined data
Visscher & Goddard (1995)[4]		0.05±.01	0.07±.02	0.07±.02	0.07±.02	0.03±.01	19 269	SM	REML	Holstein cows
		0.22±.06	0.21±.06	0.13±.05	0.14±.05	0.06±.03	8 768			Jersey cows
Visscher & Goddard (1995)[5]	0.03±.00[6]	0.03±.00[6]	0.02±.00[6]	0.02±.01	0.03±.01		37 247[7]	SM	REML	Holstein cows
	0.07±.01	0.08±.02	0.04±.01	0.02±.01	0.03±.01		10 798[7]			Jersey cows
Brotherstone *et al.* (1997)			0.08	0.08	0.03		25 227	SM	REML	registered HF cows
Jairath *et al.* (1998)	0.03	0.03	0.03				1 330 987	AM	REML	Holstein, combined data

Boettcher *et al.* (1999a)	0.04	0.05	0.04	699 722	Linear SM	REML	Canadian Holstein cows
	0.07	0.07	0.07	674 404	Threshold SM	Gibbs sampling	
			0.09	±130 000	Weibull SM	Survival analysis	restricted 305 days
			0.12	±130 000			unrestricted 305 days

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[1] probability of survival from i to i + 1 year post first calving

[2] corrected to an underlying normal scale by method of Van Vleck (1972)

[3] Approximate standard errors were ≤ .01

[4] stayabilities until lactation i

[5] probability of survival from lactation i to i + 1

[6] Standard error of .00 means < .005

[7] smallest number of cows given; numbers are: i = 1, 190,830 and 41,965; for i = 2, 164,911 and 43,824; for i = 3, 104,702 and 28,704; for i = 4, 63,940 and 18,159; and for i = 5, 37,247 and 10,798; for Holstein and Jersey cows respectively

SM = sire model; AM = Animal model

Table 2.3 Literature heritability estimates (± SE), number of records, statistical models and methods used, corrections made and remarks of analyses of functional (corrected) lifetime traits

	Estimates									
Author	**FHL**	**FLPL**	**FTMP**	**FNDL**	**FNLC**	**Records**	**Model**	**Method**	**Correction**	**Remarks**
Rogers *et al.*		0.02				5 622	SM	REML	linear and	Jersey, grade cows
(1991a)		0.04				26 034			quadratic first	Jersey, registered cows
		0.03				31 992			lactation yield	Jersey, combined data
Boldman *et al.* (1992)	0.03					53 830	SM	REML	linear within herd last lactation yield	Holstein grade cows
Short & Lawlor	0.04[1]					45 515	SM	REML	within herd	Holstein grade cows
(1992)	0.08[1]					80 126			first lactation	Holstein registered cows
	0.06[1]					125 887			yield	Holstein combined data
Vollema & Groen	0.15	0.10	0.11	0.10	0.10	94 935	SM	REML	"lactation	cows born in 1978
(1996)	0.08	0.08	0.10	0.08	0.07	166 324	SM		value"	cows born in 1982
	0.04	0.04	0.08	0.04	0.04	38 957	AM			cows born in 1985
Vollema & Groen	0.09				0.08	11 558	SM	REML VCE	"lactation	cows born in 1978
(1997)	0.07				0.06	39 252			value"	cows born in 1982
Brotherstone *et al.* (1998)					0.61	22 822	AM	REML	within herd first lactation yield	registered HF cows
Dürr *et al.* (1999)		0.08				333 147	Weibull	Survival analysis	HY parity average	Holstein cows logarithmic scale
Lubbers *et al.*					0.06[2]	21 497	SM	REML VCE	first lactation	logarithmic scale
(2000)					0.05[2]	21 497	SM	REML VCE	milk yield	without time dependant
					0.07[2]	21 497	Weibull	Survival		variates. HF cows

		0.07	21 497	Weibull	analysis		time dependant variates
Strandberg & Roxström (2000)	0.07 (0.12)[3] 0.06 (0.11)[3]		534 016 534 016	Weibull	Survival analysis	peak yield deviation from HY average	Swedish Red and White fertility determined LPL
Vollema *et al.* (2000)	0.04(0.11)[3] 0.04 (0.09)[3]		118 282 252 226	Weibull	Survival analysis	"lactation value"	BW Holstein cows RW Holstein cows
Buenger *et al.* *(*2001)	0.11 0.18		169 733 169 733	Weibull	Survival analysis	yield mature-equivalent	logarithmic scale original scale
Vukasinovic *et al.* (2001)	0.06 (0.18)[3] 0.06 (0.20)[3] 0.07 (0.18)[3]		±150 000 subset data of 3 breeds	Weibull mixed Sire-, maternal grandsire model	Survival analysis	HY parity average	Braunvieh cows Simmental cows Holstein cows
Roxström & Strandberg (2002)	0.06 (0.10)[3] 0.10 (0.16)[3] 0.18 (0.29)[3] 0.25 (0.39)[3]		538 783	Weibull mixed sire, maternal grandsire model	Survival analysis	HY parity	Swedish Red and White length of PL fertility determined PL mastitis determined PL product. determined PL
Zavadilová *et al.* (2009)	0.04		58 493	AM	REML VCE	Milk production, first lactation	Zcech fleckvieh cows
Samoré *et al.* (2010)	0.06±.01		127 416	SM	REML	average milk production	Italian Brown Swiss

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[1] approximate s.e. of heritability estimates were ≤ .01
[2] approximate s.e. of heritability estimates were < .01
[3] original scale in the parentheses
FHL = functional herd life; FLPL = functional length of productive life; FTMP = functional total milk production; FNDL = functional number of days in lactation; FNCL = functional number of lactations; SM = sire model; AM = Animal model

Heritability estimates for functional herd life ranged from 0.03 to 0.15. Heritabilities of functional traits are expected to be lower than heritability of uncorrected lifetime traits because functional traits have been corrected for milk production, which is highly heritable (Vollema & Groen, 1998).

Boldman *et al*. (1992) reported a heritability estimate for functional herd life of 0.03, which is similar to the estimate of 0.03 for uncorrected herd life.

Vollema & Groen (1996) reported heritability estimates of lifetime traits that were generally higher than those of stayability traits. In general, differences between heritability estimates from the animal and sire model are minor as might be expected according to the structure of the data (Vollema & Groen, 1996).

Most of the estimated heritabilities for functional length of productive life were in the range of 0.02 to 0.08 (Table 2.3). Vollema *et al*. (2000) reported heritability estimates of 0.041 and 0.036 in a study on Black and White and Red and White Holstein cows, respectively. These estimates for functional length of productive life were much lower than the 0.072 found by Vukasinovic *et al*. (2001) in a study on Holstein cows. They also found estimates of 0.064 and 0.062 in the same study using Braunvieh and Simmental cows. These estimates for all three breeds are higher than those obtained in other studies using methods other than survival analysis. This is due to the transformation of estimated heritabilities from the unobserved log scale to the more “realistic” original scale using Taylor series expansion (Ducrocq & Casella, 1996). The estimated heritabilities on the original scale are based only on uncensored observations.

Strandberg & Roxström (2000) defined two types of length of productive life: 1) functional productive life, where all cows that were culled before the end of data capturing were considered as uncensored; 2) fertility determined productive life, where only cows that were culled for fertility problems were considered as uncensored. Sire variances for functional productive life and fertility determined productive life were estimated to 0.029 and 0.026, respectively. This corresponds to heritability estimates of 0.069 and 0.061, respectively. When transformed to the underlying scale the heritability estimates became 0.124 and 0.109, respectively. The risk of being culled for fertility determined productive life is lower than for functional productive life at any given time, which is reasonable because culling for fertility is a part of all culling. The relative risk of culling increased consistently throughout the lactation for both longevity traits.

Roxström & Strandberg (2002) stated that reasons for culling can range from reproductive and health problems to severe injury and accidents. Therefore, they have defined functional longevity into smaller components, namely; fertility-, mastitis- and production-determined length of productive life. The estimates of heritability were higher for the cause-specific traits of longevity, indicating clearer definitions of the trait.

Buenger *et al*. (2001) and Sewalem *et al*. (2005) reported heritability estimates for functional length of productive life that were much higher than estimates obtained with different methodologies. The heritability values found in this study (ranging from 0.09 to 0.14) are within the range of studies using the Weibull model. They reinforced the idea of moving from linear models towards survival models to analyze herd life traits in dairy cattle

Vollema & Groen (1996) was the only reference that considered functional total milk production. Total milk production is a direct product of longevity and production per day. The traits considered and corrected for milk production were number of days in lactation, time between birth and last test day, time between first calving and last test day and different stayability traits (months after first calving). The weighted averages of the estimates were 0.10 and 0.084, respectively. Heritability estimates decreased with increasing year of birth.

Most of the estimated heritabilities for functional number of lactations were in the range from 0.03 to 0.07.

Lubbers *et al*. (2000) found estimated heritabilities of functional number of lactations, whether on the natural scale or log scale and for both uncensored and censored data were around 0.05, consistent with previous analysis of this trait (Brotherstone *et al*., 1998). For the proportional hazard models, the estimated heritabilities on the log scale were of similar magnitude (0.07).

Samoré *et al*. (2010), in a study on Italian Brown Swiss, reported heritability estimates for functional length of productive life of 0.06 when using a multiple trait linear sire model.

Vollema & Groen (1998) found that for their data the estimated heritabilities from the linear model and the transformed estimated heritabilities from the proportional hazards model were very similar (~0.06). When the heritability estimates from the Weibull model were transformed to the original scale, the values were substantially higher than the estimates from the linear model (0.17 vs 0.05). However, care should be taken in a comparison between the two estimated heritabilities. The estimated heritability on the log scale has a standard definition, whereas the transformed heritability is an approximation which was originally derived as a tool to compute better approximations of reliabilities using standard selection index theory (Lubbers *et al*., 2000).

2.4.2 Genetic correlations

Table 2.4 presents the genetic correlations, number of records, statistical models and methods used and remarks for uncorrected lifetime traits. Most of the reported correlations were very high, around 0.98. Vollema & Groen (1996) reported a somewhat lower genetic correlation of 0.87 between uncorrected herd life and uncorrected number of lactations for cows born in 1985. In general, genetic correlations among longevity traits were high. Genetic correlations were usually higher than phenotypic correlations. Both genetic and phenotypic correlations among lifetime traits were high (>0.87).

Numerous studies deal with the relationship between survival and type traits and the results are highly dependent on the data used. Linear type traits are relatively easy to measure, and such information is generally available in a cow's first lactation and can be used to enhance direct evaluation of longevity (Weigel *et al*., 1998). Methods that use both direct information on herd life and indirect information obtained from conformation traits have been developed by Weigel *et al*. (1998) and Jairath *et al*. (1998). Both information sources can be combined into one index after being appropriately weighed depending on reliability and genetic (co)variances between conformation traits and herd life. However, both approaches use breeding values for herd life that are estimated by traditional BLUP methods which are considered sub-optimal for herd life data (Vukasinovic *et al*., 2001).

Table 2.4 Literature genetic correlations (± SE), number of records, statistical models and methods used and remarks for uncorrected lifetime traits

Author		**Traits and estimates**			**Records**	**Model**	**Method**	**Remarks**
Hoque & Hodges		**HL**	**LPL**	**NLC**	30 738	SM	Henderson III	Holstein cows
(1980)	**TMP**	0.98[2]	0.98[2]	0.98[2]				
	HL		1.0[1,2]	1.0[1,2]				
	LPL			1.0[1,2]				
Jairath *et al.*		**NDL**	**LPL**	**NLC**	82 835	SM	REML	
(1994)	**TMP**	0.99	0.98	0.97			Holstein cows	
	NDL		1.00	0.98				
	LPL			0.98				
Vollema & Groen		**HL**	**LPL**		38 957	SM	REML	Holstein cows born in 1985
(1996)	**NLC**	0.87[3]	nc					
	NDL	nc	0.99[3]					

nc = no convergence

[1] higher than 0.997 rounded to 1.0

[2] standard error of genetic correlation ranged from .001 to .098

[3] Standard error of estimates ranged from .00 to .10

Table 2.5 Literature phenotypic correlations[1] (± SE), number of records and remarks between herd life and conformation traits

Author	Traits	Correlation	Records	Remarks
Brotherstone & Hill (1991a)	surv. lact. 2[2] - rear udder width/teat placement	0.08	23 071	Holstein-Friesian cows
	surv. lact .3 - total score	0.17		
	surv. lact. 4 - total score	0.15		
Rogers *et al.* (1991b)	func.surv. lact. 1[3] - final score	0.09	47 019	Jersey cows, registered
	FPL20 - final score	0.09	32 249	
	FLPL - final score	0.12	9 819	
Boldman *et al.* (1992)	HL - dairyness	0.07	53 830	Holstein grade cows
	FHL - fore udder att./udder depth	0.07		
Short & Lawlor (1992)	AGE54 - final score	0.10[4]	45 515	Holstein grade cows
	AGE84 - final score	0.05[4]		
	LPL - final score	0.11[4]		
	FLPL - final score	0.09[4]		
	AGE54 - final score	0.20[4]	80 126	Holstein registered cows
	AGE84 - final score	0.13[4]		
	LPL - final score	0.23[4]		
	FLPL - final score	0.21[4]		
	AGE54 - final score	0.16[4]	125 887	Holstein combined data
	AGE84 - final score	0.10[4]		
	LPL - final score	0.19[4]		
	FLPL - final score	0.16[4]		

Jairath *et al.*	FHL – capacity	0.04	119 193	Holstein, combined data
(1998)	FHL – feet and legs	0.09		
	FHL – mammary system	0.20		
	FHL – rump	0.19		
Cruickshank *et al.*	FHL, THL – mammary traits	range 0.04 to 0.10	18 725	registered Guernsey cows
(2002)	teat length	-0.05		
	FHL, THL – body type traits	range -0.01 to - 0.08		
	dairy form	range 0.07 to 0.10		

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[1] Only strongest correlation per longevity trait is given
[2] Survival of lactation 2
[3] Functional survival of lactation 1
[4] Approximate standard errors were ≤ .02

Table 2.5 presents the phenotypic correlations, number of records and remarks between herd life and conformation traits. Short & Lawlor (1992) reported phenotypic correlations between first lactation yield and type traits ranging from -0.23 for udder depth to 0.28 for dairy form in the combined analysis, similar to the estimates in the registered and grade analyses.

In a study on Guernsey cows, Cruickshank *et al*. (2002) found that phenotypic and genetic correlations between conformation traits and herd life were similar in direction, although the phenotypic correlations were generally smaller. The phenotypic correlations for the mammary traits with both true and functional herd life, ranged between 0.05 and 0.10 while the estimate for teat length was -0.05. Phenotypic correlations for most of the body type traits ranged between -0.01 and -0.08 except for dairy form (0.07 and 0.10 for functional and true herd life, respectively).

In a combined analysis phenotypic correlations between yield and the herd-life traits were smaller than were genetic correlations, ranging from 0.03 for functional herd life to 0.19 for uncorrected herd life. This is in agreement with results reported by Jairath *et al*. (1998). Of the type traits, final score had the largest phenotypic correlation with herd life traits (0.10 to 0.19), followed by the udder traits.

As evidenced by moderate genetic correlations of herd life traits with some type traits, selection on some type characteristics in first parity cows may help to improve length of productive life in both registered and grade cows. Most emphasis should be placed on udder traits compared to all type traits in selection indices including type and yield traits. Feet and leg traits also have merit although low heritability estimates will make improvement from selection slow.

Results from Brotherstone & Hill (1991a) indicated that regression coefficients for type traits usually differ little form those when both linear and quadratic terms are fitted. Phenotypic correlations between type traits and survival estimated from the same linear regression analysis are small: less than 0.1 for all the linear traits, about 0.15 for total score. The authors further stated that when all the linear type traits were fitted simultaneously with yield traits, many of the partial regression coefficients were non-significant, the remaining contributors being traits of the udder. Fitting total score removes the separate contribution of most of the linear traits, the most significant exception being udder depth and teat position rear. It is clear that total score, when fitted after linear traits, removes significant variation and is a culling criterion in its own right in these herds which undertake type classification (Brotherstone & Hill, 1991a).

Table 2.6 presents the genetic correlations, number of records, methods used and remarks between herd life and conformation traits. (Only the strongest correlation is given if more than one conformation trait was analyzed). In order to remove the association between production and lifespan (defined as number of lactations), Brotherstone *et al.* (1998) considered the relationship between functional lifespan and type traits. The genetic correlations between lifespan and type traits were adjusted to account for the genetic association between lifespan and type traits influenced by production. Adjusting for the moderate negative correlation between fore udder attachment, udder depth and yield, results in an increase in the correlation between type traits and herd life. These results indicate that increased herd life is particularly associated with a stronger fore udder attachment, short teats and higher type merit scores.

For maximum genetic progress, the genetic merit of animals must be evaluated based on information that is available early in their lifetime. In genetic evaluations for herd life, it is important to accommodate incomplete herd life information when selection decisions are made (Jairath *et al.*, 1998). Besides being measured early in life, type traits are more highly heritable than longevity itself, which can be heavily influenced by management and environmental factors (Caraviello *et al.*, 2003). However, at a time when most selection is done among young sires that have a first proof for production and type traits, the reliability of proofs for longevity for these bulls is still very limited. For such animals, genetic evaluations for herd life based on correlated conformation traits may be accurate, or even more accurate, than genetic evaluations based on survival information (Boldman *et al.*, 1992).

Table 2.6 Literature genetic correlations (± SE), number of records, methods used and remarks between herd life and conformation traits

Author	Traits	Correlation	Records	Method	Remarks
Van Doormaal *et al.* (1986)	AGE17 - dairy character	0.32	236[1]	phenotypic correlations between sire proofs for stayability and corformation traits	"breeders"
	AGE30 - dairy character	0.35			
	AGE43 - final class/general appearance	0.41			
	AGE55 - final class/general appearance	0.42			
	AGE17 - dairy character	0.29	143[1]		"milkers" paying attention to conformation traits (supervised herds)
	AGE30 - dairy character	0.23			
	AGE43 - mammary system	0.20			
	AGE55 - mammary system	0.15			
Rogers *et al.* (1989)	AGE48 - strength/body depth	-0.25	173[1]	Method of Calo *et al.* (1973)	Holstein cows
	AGE54 - body depth	-0.36			
	AGE84 - teats rear view	0.18			
	HL - body depth	-0.24			
	FAGE48 - teats rear view	0.29	143[1]		both longevity and conformation traits corrected for predicted difference for milk
	FAGE54 - body depth	-0.23			
	FAGE84 - udder depth	0.27			
	FHL - udder depth	0.22			
Rogers *et al.* (1991b)	func. Surv. lact. 1[2] - final score	0.78	9 969	REML	Jersey cows, grade herds not participating in type appraisal
	FPL20 - dairy form	0.83	6 465		
	func. Surv. lact. 1 - final score, fore udder attachment, rear udder height, front teat placement	0.34	18 525	REML	Jersey cows, registered herds not participating in type appraisal
	FPL20 - udder depth	0.82	12 798		
	FLPL - fore udder attachment	1.00	4 556		
	func. Surv. lact. 1 - udder depth	0.82	47 019	REML	Jersey cows, registered herds participating in type appraisal
	FPL20 - rear udder height	0.54	32 249		
	FLPL - fore udder attachment	0.68	9 819		

Short & Lawlor	AGE54 - dairy form	0.37	45 515	REML	Holstein grade cows
(1992)	AGE84 - udder depth	0.23			
	LPL - strength	-0.27			
	FLPL - udder depth	0.39			
	AGE54 - dairy form	0.49	80 126	REML	Holstein registered cows
	AGE84 - udder depth	0.38			
	LPL - strength	0.47			
	FLPL - udder depth	0.54			
	AGE54 - dairy form	0.46	125 887	REML	
	AGE84 - udder depth	0.30			Holstein combined data
	LPL - strength	0.40			
	FLPL - udder depth	0.44			
Visscher & Goddard	surv. lact. 2[3] - dairy character	0.35±.12	19 269	REML	Holstein cows
(1995)	surv. lact. 3 - dairy character	0.28±.12			
	surv. lact. 4 - dairy character	0.24±.13			
	surv. lact. 2 - angularity	0.73±.11	8 768	REML	Jersey cows
	surv. lact. 3 - angularity	0.82±.09			
	surv. lact. 4 - angularity	0.86±.08			
Vollema & Groen	AGE - suspensory ligament	-0.34[4]	11 558	REML	Holstein cows born in 1978
(1997)	HL - subjective score for feet and legs	0.15[4]			
	NLC - subjective score for feet and legs	0.13[4]			
	FAGE - udder depth	0.35[4]			
	FHL - udder depth	0.39[4]			
	FNLC - udder depth	0.44[4]			
	AGE36 - subjective score for type	0.48[5]	39 252		Holstein cows born in 1982
	HL - subjective score for type	0.47[5]			
	NLC - subjective score for type	0.47[5]			

	FAGE36 - subjective score for type	0.47[5]				
	FHL - subjective score for type	0.46[5]				
	FNLC - subjective score for type	0.46[5]				
	AGE36 - subjective score for udder	0.70[6]		58 864		
	AGE48 - subjective score for udder	0.82[6]				combined data 1989 plus 1990
	FAGE36 - subjective score for udder	0.78[6]				
	FAGE48 - subjective score for udder	0.93[6]				
Brotherstone *et al.* (1998)	NLC - fore udder attachment	0.46		22 822	REML	registered HF cows
	NLC - type merit	0.54				
Jairath *et al.* (1998)	FHL – capacity	0.20			REML	Holstein, combined data
	FHL – feet and legs	0.23				
	FHL – mammary system	0.57				
	FHL – rump	0.19				
Weigel *et al* (1998)	LPL - dairy form	0.41		125 887	REML	combined data HF cows
	LPL - rear udder height	0.32				
	LPL - udder cleft	0.28				
	LPL - udder depth	0.24				
	LPL - teat placement	0.22				
Vollema *et al.* (2000)	FLPL - chest width	0.41		118 282 BW 252 226 RW	survival analyses	all dairy bulls. Weibull hazard model: positive value, higher risk of being culled
	FLPL - body depth	0.41				
	FLPL - udder depth	-0.38				
	FLPL - udder (overall score)	-0.33				
Cruickshank *et al.* (2002)		THL	FHL	18 725	Multiple trait REML	registered Guernsey cows
	stature (ST)	-0.26	-0.28			
	strength (SR)	-0.27	-0.29			
	body depth (BD)	-0.26	-0.29			
	udder cleft (UC)	0.15	0.14			
	udder depth (UD)	0.20	0.24			
	teat length (TL)	-0.25	-0.27			

Zavadilová *et al.* (2009)		LPL	LPLF	58 493	REML VCE	Czech Fleckvieh cows
	Wither height (Stature)	-0.23	-0.26			
	Chest width	-0.24	-0.16			
	Dairy character/strength	-0.26	-0.18			
	Rump angle	0.03	0.07			
	Body depth	-0.16	-0.23			
	Rear legs side view	0.00	-0.08			
	Hoof angle	-0.15	-0.10			
	Rear udder attachment/height	0.28	-0.08			
	Central ligament/udder support	0.11	-0.06			
	Udder depth	-0.02	0.28			
	Teat length	-0.16	-0.14			
	Teat width/placement	-0.24	-0.29			
Samoré *et al.* (2010)	FLPL – stature	-0.22±.10		127 416	Multiple trait REML	Italian Brown Swiss
	FLPL – strength	-0.07±.11				
	FLPL – body depth	-0.10±.11				
	FLPL – rump angle	0.21±.11				
	FLPL – rear legs set	-0.56±.10				
	FLPL – fore udder attachment	0.10±.11				
	FLPL – rear udder height	-0.10±.11				
	FLPL – udder cleft	0.08±.12				
	FLPL – udder depth	0.42±.10				

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[1] Number of sires
[2] Functional survival of lactation 1
[3] Survival until lactation 2
[4] Standard error of estimates ranged from 0.051 to 0.12
[5] Standard error of estimates ranged from 0.015 to 0.067
[6] Standard error of estimates ranged from 0.0072 to 0.05
BW = Black and White, RW = Red and White

The accuracy for a progeny test for herd life, combining both lifespan and type, where the maximum number of cows have both traits recorded, shows the diminishing effect of type data as the number of progeny with lifespan observations increases (Brotherstone *et al*., 1998). With 50 or more progeny records on lifespan there is little to be gained from the type traits. On the other hand, with little or no lifespan information, type classification records provide information on which to base a sire's breeding value for herd life.

Cruickshank *et al*. (2002) reported that all four body size traits (stature, strength, thurl width and body depth) had moderate negative estimates (-0.23 to -0.29) of genetic correlations with true herd life as well as functional herd life. The estimated genetic correlations between rear udder depth and herd life were the second highest of the udder traits (0.20 and 0.24 with true herd life and functional herd life, respectively). Estimates of genetic correlation between teat length and herd life, at -0.25 for true herd life and -0.27 for functional herd life, were among the highest of all conformation traits. Cruickshank *et al*. (2002) stated that true herd life and functional herd life were near equivalent traits although due to the large proportion of very small year-season groups, the adjustment of herd life by within-herd milk production was somewhat coarse. The authors belief was that more precise calculation of relative milk production may have resulted in a clearer differentiation between herd life and functional herd life.

Rogers *et al*. (1989) used standardized transmitting abilities for 14 primary linear type traits and predicted difference for type adjusted for the effects of yield and early culling. Sires with repeatabilities less than 50% were not included. Correlation between type traits and survival proofs were adjusted by the method of Calo *et al*. (1973) to give expected values equal to genetic correlations. Reported correlations between the traits that reflect body characteristics were all negative except for rump angle and angularity. Correlations between the udder traits and survival were low. Stature, strength and body depth had slightly negative correlations with survival adjusted for milk yield. Correlations between udder support and survival after adjustment for yield ranged from 0.13 to 0.28. Teats rear view and udder depth exhibited correlations that were consistent (near 0.25) over all ages. The authors stated that udder characteristics were genetically linked to survival adjusted for yield and early culling and that most type traits have little value in selection programs aimed at reducing involuntary culling in commercial dairy cattle.

Results from Rogers *et al.* (1991b) indicated that genetic correlations between udder traits and survival were all positive except for udder cleft. The importance of the genetic correlations (especially for fore udder attachment and udder depth) were very large. Continued selection pressure for improved udder characteristics appears justified in Jerseys despite indications that udder problems may be less prevalent than in Holsteins (Rogers *et al*., 1991b).

Buenger *et al.* (2001) reported the strongest relationships between conformation traits and longevity were found for udder traits, namely udder depth, fore udder attachment, suspensory ligament, and front teat placement. Foot angle also seemed to be important, whereas most of the other body traits on longevity were less important. Compared to functional productive life, in most cases, the effect of conformation traits on uncorrected productive life was more influential, except for udder depth. Correlations between survival of grade Jerseys and type traits versus survival of registered Jerseys and type traits were similar, which contrasts reported results in Holsteins (Short & Lawlor, 1992). Genetic correlations between survival and final score were also much larger in this study compared with reports from Holstein data (Rogers *et al*., 1989). The influence of the various characteristics that make up final score may differ between breeds (Rogers *et al*., 1991b).

As reported by Short & Lawlor (1992), results from the combined analysis tended to fall between registered and grades and the correlations were highest for registered cows. This is in agreement with results from Dekkers *et al.* (1994), reporting that the strongest relationships for herd life traits were associated with udder conformation and feet and legs in registered cows. According to the moderate genetic correlations of herd life traits with some type traits, the authors suggested that selection on some type characteristics in first parity cows may help to improve length of productive life in both registered and grade cows. Udder traits should receive the most emphasis of all type traits.

Visscher & Goddard (1995) reported considerably stronger genetic correlations between stayability and conformation traits for Jerseys (0.8) than for Holsteins (0.3).

Jairath et al. (1998) reported genetic correlations of conformation traits with functional herd life to be moderately high for mammary system (0.57) but lower for capacity, feet and legs, and rump (0.19 to 0.23). Conformation traits were more closely associated with functional herd life in registered herds compared to grade herds. Most of the body traits had a slightly positive relationship with functional herd life.

In the results from Vollema *et al*. (2000), due to the model that was used, a positive correlation indicated that a higher score for a trait was associated with a higher risk of being culled. The correlations between chest width and body depth with functional length of productive life (therefore involuntary culling) were positive and strong, consequently associated with a high risk of involuntary culling. Therefore, for two cows at the same production level, the risk of being culled would be for the one with the highest score for chest width and body depth. Correlations on udder traits were in agreement with results in the literature (Rogers *et al*., 1989; Short & Lawlor, 1992).

Weigel *et al*. (1998) reported that udder traits (0.24 to 0.32), teat placement (0.22), and dairy form (0.41) had the largest correlations with length of productive life, which was consistent with the results of previous studies using independent data (Boldman *et al*., 1992). Udder traits have an important influence on involuntary culling decisions, mainly because of their influence on susceptibility to injuries and mastitis infections.

In a study on Czech Fleckvieh cows by Zavadilová *et al*. (2009), body measurements negatively correlated with length of productive life as well as functional length of productive life were wither height (stature), chest width, dairy character (dairy strength) and body depth. The correlations for wither height and body depth were almost similar for both longevity traits. Concerning the mammary traits, rear udder attachment and central ligament (udder support) showed positive genetic correlations with length of productive life, while the genetic correlation for udder depth was negative and low (-0.02). In contrast, the genetic correlations with functional length of productive life for rear udder attachment and central ligament were negative and lower as with length of productive life. The genetic correlation between udder depth and functional length of productive life was positive (0.28) and higher as with length of productive life.

Results from Samoré *et al*. (2010), in a study on Italian Brown Swiss, indicated that cows with higher stature, greater strength, deeper body and more angularity had a short herd life. Low to moderate negative genetic correlations (-0.07 to -0.22) were reported for most of the structural type traits, except for rear legs set (-0.56). Rump angle was positively correlated with functional length of productive life (0.21). Most of the udder traits were positively correlated with functional length of productive life, with a strong correlation of 0.42 for udder depth.

2.5 Summary

Ideally, survival from birth to culling or censoring provides the most accurate measure of herd life. This requires that culling dates are known. However, in South Africa culling dates were not accurately recorded for the data considered in the current study. In many instances, a dry off date may not be distinguished from a culling date. Therefore, in the current study herd life was defined as a genetically distinct survival trait in each of the first three lactations due to limitations imposed by the available data. The same definition of herd life is used in the Australian and Canadian National Genetic evaluation for herd life (Sewalem *et al*., 2007). While the survival analysis is theoretically a more appropriate model for analysis of herd life a linear model was used in the current study.

Chapter 3

Genetic parameter estimates for functional herd life for the South African Jersey breed using a multiple trait linear model[1]

3.1 Introduction

In South Africa, as in most other countries, dairy cattle breeding programs were mainly focused towards yield traits. In the last decade interest has increased in broadening the breeding objective to include other traits such as fertility, health and herd life (Miglior, 2005; Sewalem *et al.,* 2008).

Longevity or herd life of dairy cattle, a measure of success of the cow to delay the risk of involuntary culling, is a trait of considerable economic importance. Increased herd life is associated with decreased culling and therefore with decreased costs for raising or purchasing replacement heifers (Boettcher *et al*., 1999a). In addition, increased herd life is associated with increases in mean production of the herd because a greater proportion of the culling decisions are based on production, resulting in a higher proportion of matured cows in the population.

Herd life can be measured in different ways and genetic evaluations are not standardized across countries. In most countries taking part in the international bull evaluation service (INTERBULL), survival analyses is being used to estimate direct herd life (Ducrocq & Sölkner, 1998). In Australia and Canada, survival in each of the first three lactations is recorded as a binomial trait and evaluated with a multi-trait linear animal model in which survival in each lactation is considered as a different trait (Madgwick & Goddard 1989; Jairath *et al*., 1998). Despite these differences, all models of evaluation aim to assist in selecting for the same aggregate genotype of lifetime profitability (Boettcher *et al*., 1999a).

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[1] This chapter forms part of a peer-reviewed article published in the South African Journal of Animal Science. *S. Afr. J. Anim. Sci.* **39** (1), 40 – 44

Many studies have incorporated adjustments for production in models for genetic analysis of herd life and is referred to as functional herd life (Short & Lawlor, 1992; Dekkers *et al.,* 1994; Duqrocq, 1994). Dekkers (1993) reported that, although functional herd life (FHL) is not equivalent with the ability to withstand involuntary culling, use of genetic evaluations based on FHL has advantages over the use of unadjusted herd life for genetic improvement of cows for profitability. Culling decisions are made within herds and therefore the correction for production has to be on a within-herd basis (Vollema & Groen, 1996).

The approach of linear model analysis may not represent the most statistically appropriate procedure. Boettcher *et al.* (1999a) compared some of the properties of a linear model to other procedures that are more appropriate in theory (e.g. threshold model and survival analysis). However, genetic evaluation with a survival analysis may have some disadvantages relative to the linear model (Boettcher *et al.*, 1999a). One potential drawback is that computing requirements tend to be greater, both in terms of memory and time. This factor may limit genetic evaluation with survival analysis to a sire model rather than an animal model. Animal models are normally used for genetic evaluation of production traits and are preferred over sire models because they account for nonrandom mating. Because herd life receives much less emphasis in selection compared to production, nonrandom mating with respect to herd life is likely to be less common than for production, for which selected mating is often practiced (Boettcher *et al.*, 1999a).

A second potential drawback of the survival analysis is that the common approach based on days of productive life assumes that survival is the same genetic trait throughout life (Boettcher *et al.*, 1999a). As reported by Jairath & Dekkers (1994) and Boettcher *et al.* (1999a), results indicated that genetic correlations between survival in lactations 1, 2 and 3 were less than unity. Genetic effects could be modeled as time dependent covariates or perhaps with random regression approaches (Jamrozik *et al.*, 1997), but the application of such a model may be difficult (Boettcher *et al.*, 1999a).

When comparing estimated heritabilities, one must consider that the traits evaluated by the linear model versus survival analysis are slightly different (Boettcher *et al.*, 1999a). First, the linear model accounts for only variability in survival from one lactation to another. Survival analysis on the other hand is based on variability in the number of days survived across a lifetime. The ability to survive from a specific lactation to the next may be economically more important than surviving additional days within a lactation. The start of a new lactation occurs with the birth of a calf as a potential replacement heifer and increased production caused by maturity. Secondly, the trait evaluated with survival analysis was a measure of herd life across three lactations. The estimate for the linear model was the mean of three separate measures within discrete lactations (Boettcher *et al.*, 1999a).

Despite the economic significance of herd life, there is currently no genetic evaluation for herd life of dairy cattle in South Africa. A prerequisite to implementation of a genetic improvement program is the estimation of genetic parameters for traits to be improved. The primary objective of the current study was to estimate genetic parameters for functional herd life for the South African Jersey breed using a multiple trait linear approach. The secondary objective was to compare estimates of genetic parameters from the linear sire and animal models.

3.2 Materials and Methods

Data and pedigree records on purebred Jersey cows that participated in National Milk Recording and Improvement Scheme were obtained from the Integrated Registration and Genetic Information System (INTERGIS). The original data included test-day and lactation yields from 252 629 Jersey cows born between 1968 and 2005 from 2 028 herds sired by 5 394 sires. There were 4 189 393 test-day records in the original data file. Preliminary edits to ensure quality of records were conducted on the data. The editing criteria employed in the national evaluation for milk production traits for the Jersey breed were used since functional herd life is considered in the current study. For example, the following records were excluded from the analysis: (1) test-day milk yield < 1 kg or > 70 kg, fat yield < 2% or > 9%, and protein yield < 2% or > 6%, (2) first test exceeding 75 days, (3) at least one interval between test dates exceeding 100 days, and (4) records with more than one test date interval between 60 and 100 days.

The following further edits were employed: (1) first lactation records terminated before 01 January 1989 were excluded because records prior to this date comprised only completed lactations without test-day records, (2) only lactations less or equal to 305 days were considered,

(3) records with incorrect herd code, yields equal to zero and records out of specified age range were excluded; the allowable age ranges were as follows: 17 to 40, 29 to 53, and 41 to 67 months for first, second, and third calving, respectively, (4) records with unknown registration status were excluded, and (5) a first parity record was required for all cows. Furthermore, records from cows with unknown sires were excluded. A summary of the records excluded due to specific criterion is provided in Table 3.1. After editing, 181 269 cow records from 636 herds recorded over 16 years were available for analysis. All known pedigrees were used in the analyses.

Table 3.1 The editing criteria, numbers and proportions of records excluded from the analyses of herd life in the SA Jersey population

Type of edit	**Records removed**	**% Removed**
First lactation records terminated before 01 Jan 1989	632 794	15.105
Lactation length exceeded 305 days	560 867	13.388
Records with incorrect herd code	637	0.015
Records with yield equals 0	150 092	3.583
Records out of age range	91 145	2.176
Records with unknown status	416	0.010
Records outside yield range	36	0.001
Records with first test date > 75 days	22 995	0.549
Records with intervals between test dates > 100 days	8 158	0.195
Records with > one interval between 60-100 days	18 368	0.438
Records with unknown sires and dams born after 2004	326 602	7.796
Records for cows without parity 1	85 305	2.036

Survival in the first three lactations on cows that calved from 1 January 1989 to 31 December 2004 were used for parameter estimation. An observation for herd life was created as follows. Survival to the next lactation was determined based on the presence or absence of a subsequent lactation. Survival in a given lactation was treated as a binary trait and coded 1 if the cow survived during that lactation, 0 if the cow was culled during that lactation or the number of days between the current calving and extraction date exceeded 581 days. Records from cows where the number of days between current calving date and data extraction date were less than 581 days were considered as records in progress and were excluded from the analysis. The value 581 was calculated as mean calving interval plus three standard deviations to ensure each cow had enough opportunity to calf if it was still in the herd. The criteria used to determine survival is further explained in Table 3.2.

Table 3.2 Criterion used to create survival observations[1] for analysis of herd life in the South African Jersey breed

Item	**Survival in lactation**		
	1	**2**	**3**
Survived lactation 3	1	1	1
Culled in lactation 3	1	1	0
Culled in lactation 2	1	0	-
Survived lactation 1	1	-	-

[1] Survival is coded as 1 if a cow survived and 0 otherwise, the symbol "–" indicates that survival could not be determined (i.e. records in progress). Survival was determined as follows: for lactation *n*; survival = 1 if there was lactation *n*+1, and survival = 0 if there was no lactation *n*+1 and the number of days between current calving date and data extraction date exceeds 581 days. Survival is undefined (-) if the number of days between current calving date and data extraction date is less than 581 days.

Survival rate per lactation is summarized in Table 3.3. Survival rate was 72.4, 71.6, and 67.4% for lactations 1, 2 and 3, respectively.

Two mixed linear models were used to estimate (co)variance components for survival i.e. three-trait sire and animal models.

Table 3.3 Survival rate per lactation for the first three lactations in the SA Jersey population

Lactation	**N**	**N_{surv}**	**Survival rate**	
			Within lactation (%)	**Across lactation (%)**
1	90 530	65 544	72.4	72.4
2	56 854	40 708	71.6	44.9
3	33 885	28 839	67.4	25.2

N = number of cows; N_{surv} = number of cows surviving per lactation

The three-trait sire model can be presented as follows:

$$Y_{ijkl} = hy_{il} + rhs_{jl} + (age_k)_l + (prot_k \times rhs_j)_l + (prot_k)_l + (fat_k)_l + sire_{kl} + e_{ijkl} \quad [1]$$

where Y_{ijkl} = observation for survival (0 or 1) in lactation *l* (*l* = 1, 2, and 3) on cow *k* that calved in herd-year *i*;

hy_{il} = fixed effect of herd-year *i* for lactation *l*;

rhs_{jl} = fixed effect of subclass *j* for registry status×herd size change×season of calving for lactation *l*;

$(age_k)_l$ = linear and quadratic regressions of survival in lactation *l* on age at first calving;

$(prot_k \times rhs_j)_l$ = linear regression of survival in lactation *l* on $prot_{kl} \times rhs_{jl}$ subclasses, where $prot_k$ is the normalized deviation of 305-day protein yield within herd-year average in first lactation, for a daughter of sire *k*;

$(prot_k)_l + (fat_k)_l$ = linear, quadratic, and cubic regressions of survival in lactation *l* on normalized deviation of 305-day protein and fat yield within herd-year average in first lactation;

$sire_{kl}$ = random genetic effect of sire *k*;

e_{ijkl} = random residual.

The following distributional assumptions were made about the random effects; $\mathbf{s} \sim N(\mathbf{0}, \mathbf{A}\sigma_s^2)$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ where $\mathbf{s}$ is a vector of sire additive genetic effects and $\mathbf{e}$ is a vector of residual effects. The σ_s^2 and σ_e^2 are the sire and residual variances, respectively. The **A** is the Wright's numerator relationship matrix and **I** is an identity matrix. The animal model was similar to equation [1] except that the sire genetic effect was replaced by the animal additive genetic effect. The animal genetic effects were assumed to be normally distributed with (co)variance structure $\mathbf{A}\sigma_a^2$ with σ_a^2 being the animal additive genetic variance.

A minimum of 10 cows sired by at least 2 sires was required per herd-year of calving to ensure connectedness in the data, and to reduce the bias caused by preferential treatment of daughters of a particular sire in a particular herd or group of herds. Records of cows from herd-year subclass without variation were excluded from the analysis. Registration status was defined in 2 classes; cows in herds with registered cows, and cows in herds with non-registered cows. Three classes for change in herd size were defined based on the percentage of change from one year to the next (decreasing = for a decrease in herd size of <-5%; nearly unchanged = no appreciable change ≥-5% to ≤10%; and increasing = for increases in herd size of >10%).

The original data set including all the cows was used when creating the registration status and herd size change classes. Similar to Mostert *et al.* (2004), two seasons of calving were defined as Winter (from April to September) *versus* Summer (from October to March). The same procedure is used in the current national genetic evaluation for the Jersey breed. The first lactation yield for protein and fat were used because genetic correlation between first lactation yield and yield in later lactations is high. Furthermore, low yield in the terminal lactation could have been caused by a health problem, which is what functional herd life attempts to measure (Short & Lawlor, 1992).

(Co)variance components were estimated fitting a multiple-trait sire and animal model using the VCE5 package of Groeneveld (1994). Heritability for the sire model was calculated using $h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_e^2}$. The standard errors of the heritability estimates were computed using the delta method of Searle *et al.* (1992).

3.3 Results and Discussion

Estimates of heritability and genetic correlations for survival in the first three lactations from the multiple-trait sire and animal models are presented in Tables 3.4 and 3.5, respectively. Heritability estimates from both models were approximately similar for all lactations. However, the heritability estimates for lactations 2 and 3 were slightly higher with the sire model compared to the animal model. When lowly heritable traits such as herd life are analyzed with an animal model, most information comes from the sire component and the difference between sire and animal models is expected to be small (Vollema & Groen, 1996). Estimates of heritability were in the range of 0.02 to 0.03, which are comparable but on the lower end of previously published estimates of approximately 0.04 (Short & Lawlor, 1992; Jairath & Dekkers, 1994). Boettcher *et al*. (1999a) reported estimated heritabilities of approximately 0.07 for all lactations on the underlying scale with the threshold model and in the order of 0.08 with the survival analyses.

Table 3.4 Heritability (s.e.) (on the diagonal) and genetic correlation (s.e.) (above the diagonal) estimates of survival in the SA Jersey population obtained from a multiple-trait sire model

Lactation	**Lactation**		
	1	**2**	**3**
1	0.03±0.01	0.99±0.04	0.68± 0.11
2		0.02±0.01	0.70±0.12
3			0.03±0.01

The genetic correlation between lactations 1 and 2 from both the sire and animal models was higher than that between lactations 2 and 3. The lowest correlation was between lactation 1 and 3 for both models. Boettcher *et al*. (1999b) also reported similar results using data on Canadian Holsteins. These results suggest that the genetic factors that determine survival are slightly different in first and the third lactation. Genetic correlations from the sire model ranged from 0.68 to 0.99. This range is similar to results (0.84 to 0.91) reported by Boettcher *et al*. (1999a) and by Short & Lawlor (1992). Jairath & Dekkers (1994) observed genetic correlations that were only moderately high (0.60 to 0.75), while Visscher & Goddard (1995) reported estimates between 0.91 and 0.97 for Holstein-Friesians and Jerseys.

Table 3.5 Heritability (s.e) (on the diagonal) and genetic correlation (s.e) (above the diagonal) estimates of survival in the SA Jersey population obtained from a multiple-trait animal model

Lactation	**Lactation**		
	1	**2**	**3**
1	0.03±0.01	0.99± 0.01	0.76±0.09
2		0.01±0.01	0.82±0.09
3			0.02±0.01

In the current study a linear model was used because it is easy to implement and previous research has shown that the difference in heritability estimates expressed on the underlying scale is negligible when linear and non-linear models are used for analysis of binary traits (e.g. Boettcher *et al*., 1999a).

3.4 Conclusions

Results from the current study suggest that genetic variation exists for herd life to allow for genetic improvement through selection, although the response to selection could be slow due to the low estimates of heritability. The moderate positive genetic correlation between survival in the first and third lactation suggest that early selection for functional herd life is feasible.

Chapter 4

Correlated response in longevity from direct selection for production in the South African Jersey breed[2]

4.1 Introduction

Longevity or herd life is of major economic importance in dairy cattle production (Boettcher *et al*., 1999a; Settar & Weller, 1999). Herd life can be measured in a variety of ways, and genetic evaluations are not standardized across countries. However, its heritability is low, and herd life is expressed at a later age than traits used in the current South African Jersey selection program.

Increased herd life affects overall profitability of milk production by reducing replacement costs and increasing the proportion of mature, high producing cows in the herd. It also enables a greater selection response, because fewer cows have to be replaced and, therefore higher selection intensity of cows is possible (Vukasinovic *et al*., 2001). Selection for herd life is hampered by the time required for cows to have complete records. For maximum genetic progress, genetic merit of cows must be evaluated based on information that is available early in the lifetime of the animal. It therefore follows that genetic evaluation for herd life must be able to utilize incomplete herd life information on cows that are still in the herd when selection decisions are made (Jairath *et al*., 1998).

As a result, most national genetic evaluation programs for dairy cattle include breeding values for herd life (Miglior *et al*., 2005; Forabosco *et al*., 2008). Different definitions for herd life have been considered in dairy cattle in several countries leading to different models implemented in national genetic evaluation for herd life (Sölkner & Ducrocq, 1999; Veerkamp *et al*., 2001; Caraviello *et al*., 2004). These definitions are based either on the number of parities or

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[2] This chapter forms part of a peer-reviewed article published in the South African Journal of Animal Science. *S. Afr. J. Anim. Sci.* **42** (1), 38 – 46

the actual length of herd life (Vollema & Groen, 1996). Furthermore, genetic differences for milk yield will have a major effect on direct measures of survival, because low milk yield is a major cause of cow culling (Settar & Weller, 1999). Many studies have proposed analyzing functional herd life, which is generally computed as herd life adjusted for milk yield (Jairath *et al*., 1998; Settar & Weller, 1999). This trait is independent of production and reflects the fertility, health, and overall fitness of the cow. In the present study functional herd life was defined as survival in the first three lactations with survival in each lactation considered genetically correlated traits. Du Toit *et al*. (2009) found genetic correlations ranging from 0.68 to 0.99 between survival adjusted for production within each of the first three lactations. Jairath & Dekkers (1995) reported genetic correlations among survival in the first three lactations that were only moderately high (0.60 to 0.75), indicating that survival was a different genetic trait in each lactation. Boettcher *et al*. (1999a) reported estimates that were higher (0.84 to 0.91). To accommodate these differences, the Canadian genetic evaluation system models survival as different traits in the first three lactations, assigning cows to different contemporary groups for each subsequent calving.

Prior to the implementation of longevity in most genetic evaluation systems selection was mainly dominated by production traits. Vollema & Groen (1997) reported high genetic correlations between 305-day milk production in first lactation and uncorrected longevity traits (0.45 to 0.74). Genetic correlations between functional longevity traits and milk production were much lower (0.09 to 0.20). Short & Lawlor (1992) reported a genetic correlation of 0.44 between milk yield and herd life, with a genetic correlation of 0.08 between milk yield and functional herd life. It is worthwhile to investigate whether selection for production has resulted in undesirable response in longevity.

The objective of the current study was to investigate whether direct selection for production resulted in an undesirable genetic response in functional longevity in the South African Jersey breed.

4.2 Materials and methods

Performance and pedigree records of South African registered Jersey cows that participated in the National Milk Recording and Improvement Scheme were obtained from the South African national livestock database commonly known as the Integrated Registration and Genetic Information System (INTERGIS). Data used in the current study (before editing) included production records from 245 134 Jersey cows from 2 004 herds. These cows were progeny of 5 364 sires and 124 868 cows and were born between 1968 and 2005.

Observations for functional herd life were derived as follows: Survival in a given lactation was determined based on the presence or absence of a subsequent lactation. Survival was treated as a binary trait and coded 1 if the cow survived and 0 if the cow was culled or the number of days between the current calving date and extraction date exceeded 581 days. Records from cows where the number of days between current calving date and data extraction date were less than 581 days were considered as records in progress and were excluded from the analysis. The value 581 was calculated as mean calving interval plus 3 standard deviations (mean ± SD values) to ensure each cow had enough opportunity to calve if it was still in the herd (Du Toit *et al.*, 2009). The criteria used to determine survival are explained in Table 4.1.

Table 4.1 Criteria used to derive survival observations[1] for analyses for functional herd life in the South African Jersey breed

Item	**Survival in lactation**		
	1	**2**	**3**
Survived lactation 3	1	1	1
Culled in lactation 3	1	1	0
Culled in lactation 2	1	0	-
Survived lactation 1	1	-	-

[1] Survival is coded as 1 if a cow survived and 0 otherwise, the symbol "–" indicates that survival could not be determined (i.e. records in progress). Survival was determined as follows: for lactation *n*; survival = 1 if there was lactation *n*+1, and survival = 0 if there was no lactation *n*+1 and the number of days between current calving date and data extraction date exceeds 581 days. Survival is undefined (-) if the number of days between current calving date and extraction date is less than 581 days.

The editing criteria employed in the official national evaluation for production traits for the Jersey breed were used. Specifically, the following records were excluded from the analysis: (1) test-day milk yield < 1 kg or > 70 kg, fat percentage < 2% or > 9%, and protein percentage < 2% or > 6%, (2) the interval between calving and first test day exceeding 75 days, (3) at least 1 interval between test dates exceeding 100 days, and (4) records with more than one test date interval between 60 and 100 days. Furthermore, (1) first lactation records terminated before 01 January 1989 were excluded because there were only few cows with test-day records prior to 1989, (2) records with incorrect herd code and records outside specified age range were excluded; the allowable age ranges were as follows: 17 to 40, 29 to 53, and 41 to 67 months for first, second, and third parity, respectively, and (3) records with unknown registration status were excluded. A summary of the records excluded due to specific criteria is provided in Table 4.2. Most of the records were deleted mainly due to first lactations being terminated before 01 January 1989 (15.1%), followed by records with yield equals 0 (3.6%) and records out of age range for the first three parities (2.2%).

Table 4.2 Numbers and proportions of records excluded from the analyses for functional herd life in the SA Jersey breed

Type of edit	**Number of records removed**	**% of records removed**
First lactation records terminated before 01 Jan 1989	615 323	15.117
Records with incorrect herd code	637	0.016
Records with yield equals 0	148 454	3.647
Records out of age range	87 580	2.152
Records with unknown status	416	0.010
Records outside yield range	33	0.001
Records with first test date > 75 days	21 853	0.537
Records with intervals between test dates > 100 days prior to 305 days of lactation	7 173	0.176
Records with more than 1 interval between 60-100 days	17 894	0.440
Total number of records excluded	899 363	22.096

After editing, the data comprised 125 896, 84 133 and 52 833 cows with 1^{st}, 2^{nd} and 3^{rd} lactation herd life observations. These cows were daughters of 3 736 sires. A total of 963 herds were represented in the data. The minimum and maximum number of daughters per sire was 1 and 3 899, respectively, with a mean of 30 daughters per sire. Summary statistics of the edited data are provided in Table 4.3.

A three-trait mixed linear animal model was used to estimate breeding values for survival. A matrix representation of the models for survival in each of the three lactations is as follows:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Za} + \mathbf{ZQg} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of observations, $\boldsymbol{\beta}$ is a vector of fixed effects, $\mathbf{a}$ is a vector of random additive genetic effects, $\mathbf{g}$ is a vector of genetic group effects and $\mathbf{e}$ is a vector of random residuals. $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices relating fixed and random effects respectively to observations; $\mathbf{Q}$ is an incidence matrix that relates animals to genetic groups. The following distributional assumptions were made about the random effects: $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma^2_a)$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{R}\sigma^2_e)$. The σ^2_a and σ^2_e are the animal additive genetic and residual variances, respectively. The $\mathbf{A}$ is the Wright's numerator relationship matrix and $\mathbf{R}$ is a residual matrix.

Table 4.3 Summary statistics of the edited data used for the analyses of herd life in the SA Jersey population

Item	N	Mean	Standard deviation	Minimum	Maximum
Age at first calving (months)	125 896	26.31	3.96	17.00	40.00
Fat yield in first lactation (standardized)	125 896	0.50	1.02	-5.00	5.00
Protein yield in first lactation (standardized)	125 896	0.50	1.02	-5.00	5.00
Survival in lactation 1	125 896	0.75	0.43	0.00	1.00
Survival in lactation 2	84 133	0.74	0.44	0.00	1.00
Survival in lactation 3	52 833	0.71	0.45	0.00	1.00

The fixed effects considered in the model were herd×year, registry status×herd size change×season (RHS), age at first calving (linear and quadratic regression), linear regression on normalized deviation of 305-day protein yield in lactation 1 within RHS, linear, quadratic, and cubic regressions on normalized deviation of 305-day protein and fat yields. Fixed effects were defined as follows: Registration status was defined in 2 classes; namely, cows in herds with registered cows, and cows in herds with non-registered cows. Three classes for change in herd size were defined based on the percentage of change from one year to the next (decreasing = for a decrease in herd size of <-5%; nearly unchanged = no appreciable change ≥-5% to ≤10%; and increasing = for increases in herd size of >10%). Similar to Mostert *et al*. (2004), two seasons of calving were defined as Winter (from April to September) *versus* Summer (from October to March). The first lactation protein and fat yields were used because the genetic correlation between first lactation yield and yield in later lactations is high. Furthermore, low yield in the terminal lactation could have been caused by a health problem, which is what functional herd life attempts to measure (Short & Lawlor, 1992).

A pedigree file used in the current study to account for relationships among animals included all cows with observations and their ancestors (n = 456 355) and genetic groups (n = 69). A genetic group was defined as a concatenation of country of origin, year of birth, and selection path (e.g. sire of sire, sire of dam, dam of sire and dam of dam). Table 4.4 shows the levels of the fixed and random effects considered in the current study.

Table 4.4 Levels of fixed and random effects included in the model for analysis of herd life in the SA Jersey population

Item	**Number of levels**		
	Lactation		
	1	**2**	**3**
Fixed effects			
herd×year	4 991	3 760	2 726
registry status×herd size change×season (RHS)	16	17	17
305-day protein yield in lactation 1 within RHS	143	125	122
age at first calving	1	1	1
fat (linear)	1	1	1
fat (quadratic)	1	1	1
fat (cubic)	1	1	1
protein (linear)	1	1	1
protein (quadratic)	1	1	1
protein (cubic)	1	1	1
Random effects			
animal	456 424	456 424	456 424

The (co)variance components used in the current study were derived from estimates obtained from a multiple-trait sire model by Du Toit *et al.* (2009). The (co)variance components are provided in Table 4.5. The (co)variance components were derived as follows:

(1) Additive genetic variance for a given lactation using $\sigma^2_{a_i} = 4\sigma^2_{s_i}$

(2) Additive genetic (co)variance between two lactations using $\sigma_{a_i,a_j} = 4\sigma_{s_i,s_j}$ for $i \neq j$

(3) Residual variance using $\sigma^2_{e_i} = 4\sigma^2_{s_i}(1-h_i^2)/h_i^2$

(4) Residual (co)variance between two lactations using $\sigma_{e_i,e_i} = -3\sigma_{s_i,s_i} + \sigma_{E_i,E_i}$ for $i \neq j$ where E_i is the residual from a sire model.

Table 4.5 (Co)variance components ($\times10^{-3}$) and heritability estimates used in genetic evaluation of longevity in the South African Jersey breed

Item	**Lactation**		
	1	**2**	**3**
Additive genetic (co)variances	5.12	4.29	3.31
		3.69	2.92
			4.68
Residual (co)variances	146.25	-0.69	-5.32
		164.89	-2.79
			176.87
h^2	0.034	0.022	0.026

Estimated breeding values (EBVs) were obtained using PEST (Groeneveld, 1994). Estimates of breeding values for lactations 1, 2 and 3 were obtained from solving the mixed model equations. The three EBVs were assumed to be equally important and combined into a single breeding value as $\mathrm{EBV}_L = (\mathrm{EBV}_1 + \mathrm{EBV}_2 + \mathrm{EBV}_3)/3$. Therefore, the EBV for longevity in the current study is an indication of the ability of a sire's daughters to survive the first three lactations. This approach is similar to that used in the Canadian genetic evaluation in Holsteins (Boettcher *et al.*, 1999b).

The scale or unit of the breeding values is unknown when using a linear sire model. To present the breeding values on a desired scale, the breeding values were standardized by using the mean and standard deviation of the base group. The base group was defined as proven sires born between the years 1990 and 2000 inclusive. The standardized breeding values were then expressed as relative breeding values by using the mean of 100 and standard deviation of 5, similar to the procedure used by Van der Linde *et al.* (2007).

Accuracies were computed following the method of Liu *et al.* (2004):

$$R^2 = \frac{n_{ei}}{(n_{ei} + k)}$$

where $k = \frac{(4-h^2)}{h^2}$ and n_{ei} is the effective number of daughters for sire *i*. The effective number of daughters was computed as follows (Fikse & Banos, 2000):

$$n_{ei} = n_{ti} - \sum_j \frac{n_{ij^2}}{n_j}$$

where n_{ti} is the total number of daughters of sire *i*, n_{ij} is the number of daughters of sire *i* in contemporary group *j*, n_j is the size of contemporary group *j*, and summation is over all the number of contemporary groups that sire *i* has daughters. This method is considered standard in dairy cattle genetic evaluation systems.

The criteria for official publication of breeding values for proven sires were as follows: (1) sires were required to have at least one daughter with an observation for herd life, (2) a minimum of 20 daughters in 10 herds with milk production records. A total of 559 sires met the criteria for publication.

Genetic trend for sires that met the criteria for publication was obtained by regressing the mean breeding value on year of birth of these sires.

4.3 Results and Discussion

The distribution of the EBV's for the proven sires is presented in Figure 4.1. The mean and standard deviation of the breeding values of these sires was 99 and 5, respectively. These values were similar to the assumed mean and standard deviation of 100 and 5, respectively. The range of the breeding values was 79 to 114.

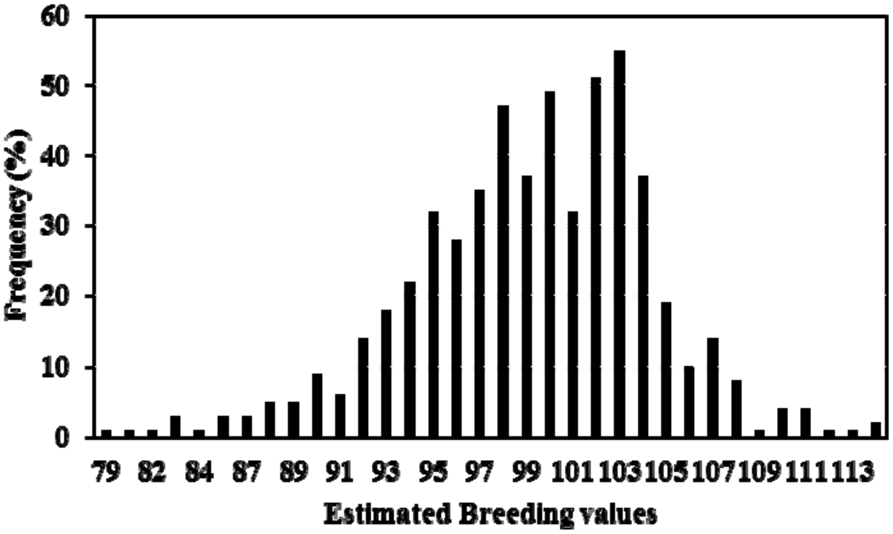

Figure 4.1 Distribution of estimated breeding values for functional herd life for all proven sires (N = 559) in the South African Jersey breed

Different expressions of nationally predicted sire breeding values for herd life exist in other countries. Canadian bull proofs on Holsteins for combined herd life are expressed in terms of Relative Breeding Values (RBVs) using a scale with an average of 100 and a range of 85 (undesired) to 115 (desired) to include 99 % of all proven sires (Van Doormaal, 2010). Boettcher *et al*. (1999b) expressed the results of bulls for combined herd life as expected transmitting abilities (ETA) for the number of lactations that daughters are expected to survive, after adjustment for production, standardized to a base of 3 lactations. The EBV ranged from 2.22 to 3.40 with a standard deviation of 0.15. Using a similar procedure, Jairath *et al*. (1998) reported a standard deviation of ETA of 0.156 lactations, and the range was from 2.31 to 3.43 lactations. In the national genetic evaluation of Holsteins in the Netherlands EBVs for functional herd life were expressed as a relative breeding value with a mean of 100 and a genetic standard deviation of 4.5. Due to trait definition and expression of the breeding value for herd life, the Dutch Cattle Improvement Organization decided to exclude milk production as an effect from the model of their genetic evaluation from January 2008 onwards. The derived breeding value for productive herd life (true herd life) was expressed in days. The argument for changing from a relative to an absolute expression of the EBV for herd life was that an EBV in days clearly shows the effect of a bull on the herd life of his daughters (Van der Linde *et al*., 2007).

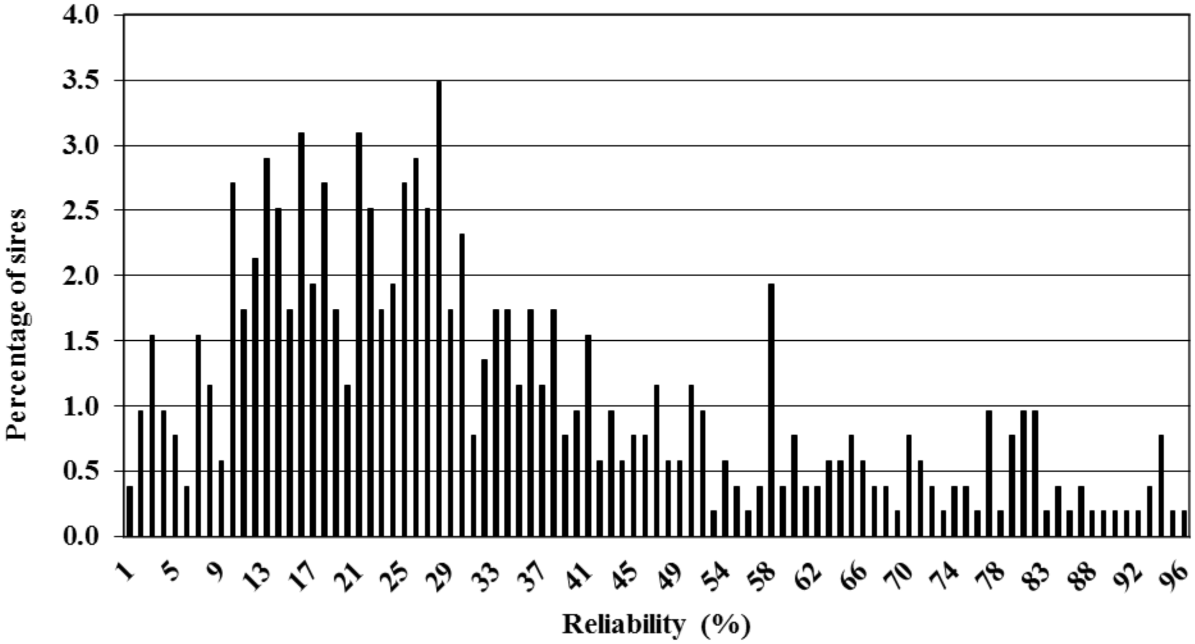

Figure 4.2 Distribution of reliabilities for all proven sires (N = 559) in the South African Jersey breed

The distribution of reliabilities among the proven sires is somewhat skewed (Figure 4.2). The mean reliability was 33.43 % with a range of 0.82 % to 95.66 %. These low reliabilities are due to insufficient numbers of daughters for a more accurate proof because of the low heritability of the trait. The Canadian criterion for an official bull proof is 65 % and 55 % reliability for production and type traits, respectively. A bull's proof for herd life is published only when the criteria for type is met.

Figure 4.3 shows the genetic trend for functional herd life for proven bulls for the period 1985 to 2002. The rate of genetic progress per year was statistically non-significant (b = 0.03 ± 0.05 per year). Similarly, Jairath *et al.* (1998) reported a slight positive trend for herd life when the means of expected transmitting ability (ETA) were plotted by year of birth.

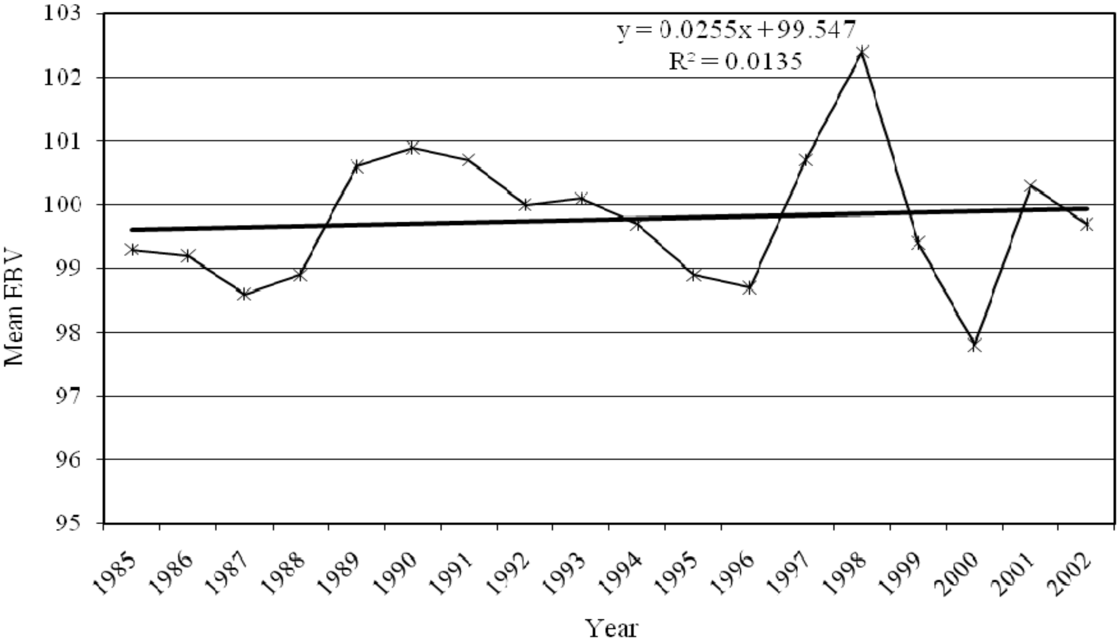

Figure 4.3 Genetic trend for functional herd life for proven sires (N = 559) in the South African Jersey breed

In the present study cows were included in the analyses if they had initiated a first lactation. Survival thereof could only be defined if there was a subsequent calving or the number of days between current calving date and data extraction date exceeded 581 days, similar to the procedure followed by Boettcher *et al.* (1999b) and Olori *et al.* (2002). This delay means that young bulls cannot be evaluated early for herd life, thus ruling out early selection decisions. A further delay is due to the time it takes to have sufficient daughters for a reliable proof because of the low heritability of the trait (Olori *et al.*, 2002).

As reported by Boettcher *et al.* (1999b) on Canadian Holsteins, registered South African Jerseys are also classified for conformation during their first lactations and functional herd life includes the first 3 lactations. Therefore most bulls, particularly recent progeny test bulls, will have more daughter information for linear type traits than for functional herd life. Thus the reliability of the proofs could be enhanced by including linear type traits in the model for evaluation of functional herd life.

4.4 Conclusions

Correlated genetic response on longevity from direct selection on production was estimated in the current study. The results indicate that direct selection for production in the South African Jersey breed did not result in undesirable genetic response in longevity. In addition, the results from the current study indicate that direct selection for longevity in the South African Jersey breed is feasible. However, it should be noted that while direct selection for functional herd life could lead to genetic progress, this genetic response could be relatively slow due to the low heritability and long generation interval.

Chapter 5

Relationships between functional herd life and conformation traits in the South African Jersey breed[3]

5.1 Introduction

Functional herd life in dairy cattle is of economic importance because longer herd life is associated with lower heifer replacement costs and a higher proportion of productive mature cows in the herd. Therefore, functional herd life is an integral part of the breeding objective for dairy cattle. Research has shown that genetic variation exists for functional herd life to allow for genetic improvement through selection (Vukasinovic *et al*., 2001; Cruickshank *et al*., 2002; Tsuruta *et al*., 2005). The challenge of using direct measures of functional herd life in the genetic improvement programme is that this trait can only be observed at the end of productive life. For maximum genetic progress, the genetic merit of animals must be evaluated based on information that is available early in their lifetime. Thus, direct genetic improvement for functional herd life may take too long. It is therefore important to identify and emphasize traits associated with herd life that are expressed early in life to allow breeders to select for profitable and functional cows.

Low to moderate genetic relationships between various conformation traits and functional (milk-corrected) herd life were reported in the literature. Specifically, the highest genetic relationships were generally found for udder attachment, udder depth, teats, and angularity of rear legs (Vukasinovic *et al*., 2002; Strapák *et al*., 2005; Bouška *et al*., 2006; Zavadilová *et al*., 2009). In a study on Quebec Holsteins, Schneider *et al*. (2003) found that udder and stature had the strongest relationships with functional herd life compared to other structural body traits. Furthermore, Bouška *et al*. (2006) reported positive relationships for particularly udder traits and herd life for Czech Fleckvieh cows. Similarly, Caraviello *et al*. (2003) found that udder depth

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[3] This chapter forms part of a peer-reviewed article published in the South African Journal of Animal Science.
S. Afr. J. Anim. Sci. **42** (1), 47 – 54

was by far the most important type trait, with respect to herd life, followed by fore udder, front teat placement, and udder support in US Jersey cows. In a study on US Holsteins, Tsuruta *et al*. (2005) found that more capacious and better attached udders, shorter teats, smaller body size, straighter legs, steeper foot angle, and higher overall conformation scores were consistently related to increased herd life.

It is evident that desirable conformation traits can positively influence the functional herd life of cows and thus the economic efficiency of the herd. Type classification data are recorded on registered cows in the South African Jersey cows since 1989, and their use as an indirect predictor for herd life will be very cost effective. Besides being measured early in life, type traits are more heritable than herd life, which can be heavily influenced by management and environmental factors (Caraviello *et al*., 2003). Genetic evaluation for herd life including correlated conformation traits may be more accurate than evaluations based on survival information alone (Boldman *et al*., 1992; Boettcher *et al*., 1997). The main objective of this study was to estimate the genetic relationships between functional herd life and conformation traits in the South African Jersey breed.

5.2 Materials and methods

Data on conformation traits on registered South African Jersey cows calving between 1989 and 2008 were obtained from the South African national database, the Integrated Registration and Genetic Information System (INTERGIS). These cows participated in the South African National Milk Recording and Improvement Scheme. For convenience, the conformation traits were grouped into body structure and udder traits (Table 5.1). Body structure traits included stature (wither height), chest width, body depth, dairy strength (a composite trait consisting of chest width, body depth and angularity), rump angle, thurl width, rear leg side view and foot angle. Udder traits included fore udder attachment, rear udder height, rear udder width, udder support (udder cleft), udder depth, front teat placement, rear teat placement and front teat length. These traits were scored only once, preferably on cows in their first lactation. After editing 80 % of the records were from cows scored in their first lactation and 20 % in their second lactation. A subjective linear scoring system ranging from 1 to 9 was used, except for foot angle with a maximum score of 8.

Data editing for conformation traits was carried out following the standard editing criteria used in the South African National Genetic Evaluation Programme for the Jersey breed. Briefly, data from cows younger than 17 months or older than 36 months of age at first calving and younger than 29 months and older than 53 months at second calving were excluded from the analyses. Cows younger than 17 months or older than 46 months when scored at first parity and those younger than 29 months and older than 63 months when scored in the second parity were also excluded from the analyses. Cows classified on days in milk less than 5 and greater than 300 days were also excluded from the analyses. Contemporary groups with at least five animals, that are progeny of at least two sires, were considered. A contemporary group was defined as a concatenation of herd-year-season-classification code and parity. Descriptive statistics of the final data set are provided in Table 5.2.

The following data were used in the analyses of herd life. A total of 4 189 393 test-day records were obtained from the INTERGIS. Functional herd life was defined as survival in the first, second and third lactation adjusted for production. Similar data were used previously in estimation of genetic parameters for functional herd life (Du Toit *et al.*, 2009). The editing criteria employed in the national evaluation for milk production traits for the Jersey breed were used. The following records were excluded from the analyses of functional herd life: (1) test-day milk yield < 1 kg or > 70 kg, fat yield < 2 % or > 9 %, and protein yield < 2 % or > 6 %, (2) first test exceeding 75 days, (3) at least one interval between test dates exceeding 100 days, and (4) records with more than one test date interval between 60 and 100 days. Further editing employed included: (1) first lactation records terminated before 01 January 1989 were excluded because records prior to this date comprised only completed lactations without test-day records, (2) lactations with less than 5 days in milk and greater than 305 days in milk were excluded, (3) records with incorrect herd code, yields equal to zero and records out of specified age range were excluded; the allowable age ranges were as follows: 17 to 36, 29 to 53, and 41 to 67 months for first, second and third calving, respectively, (4) records with unknown registration status were excluded, and (5) a first parity record was required for all cows. Furthermore, records from cows with unknown sires were excluded. Cows born after 2004 were excluded due to limited number of records. All known pedigrees were used in the analyses.

Table 5.1 Classification system for conformation traits in the South African Jersey breed

Score	1	5	9	Ideal score
Body structure				
Stature	short	intermediate	tall	6
Chest width	narrow	intermediate	wide	6
Body depth	shallow	deep	very deep	6
Dairy strength	frail	intermediate	strong	8
Rump angle	high pins	level	extreme slope	6
Thurl width	narrow	intermediate	wide	8
Rear leg side view	straight	intermediate	sickled	6
Foot angle	very low	intermediate	very steep	7
Udder traits				
Fore udder attachment	weak	intermediate	strong	8
Rear udder height	low	intermediate	high	8
Rear udder width	narrow	intermediate	wide	7
Udder support	indistinct	deep	very deep	6
Udder depth	deep	intermediate	shallow	7
Front teat placement	wide	center	narrow	7
Rear teat placement	wide	center	narrow	5
Front teat length	short	intermediate	long	5

A series of bivariate analyses, including one conformation trait and one functional herd life trait, were carried out to estimate genetic correlations between functional herd life and conformation traits. The matrix representation of the model fitted is as follows:

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

Where **y** is a vector of records, **b** a vector of fixed effects, **u** is a vector of random direct additive genetic effects and **e** is a vector of random residual effects. The fixed effects considered for conformation traits were contemporary group, age at classification (fitted as linear and quadratic), age at first calving (fitted as linear and quadratic) and days in milk (fitted as linear and quadratic). The fixed effects for functional herd life were herd-year, registry status x herd size change x season of calving (rhs), age at calving (fitted as linear and quadratic), protein within rhs, protein and fat yield deviations (fitted as linear, quadratic and cubic). **X** and **Z** are incidence matrices relating fixed and random effects with the observations. (Co)variance components were estimated using VCE6 (Groeneveld *et al.*, 2010). Estimates of genetic correlations were considered significant if the absolute value was greater than twice the standard error of the estimate.

5.3 Results and discussion

Table 5.2 presents the descriptive statistics and trait abbreviation for functional herd life and conformation traits.

Table 5.2 Descriptive statistics and trait abbreviations for functional herd life and conformation traits in the South African Jersey breed

Traits	Abbreviation	Number	Mean	SD	CV (%)	Min	Max
Functional herd life							
First lactation	FHL1	90 530	0.72	0.45	62	0	1
Second lactation	FHL2	56 854	0.72	0.45	63	0	1
Third lactation	FHL3	33 885	0.67	0.47	70	0	1
Body structure							
Stature	WH	46 237	5.40	0.82	15	1	9
Chest width	CW	22 484	5.60	0.69	12	1	9
Body depth	BD	22 484	7.03	0.78	11	1	9
Dairy strength	DS	46 238	6.63	0.80	12	1	9
Rump angle	RA	46 238	5.54	0.65	12	1	9
Thurl width	TW	46 238	5.49	0.73	13	1	9
Rear leg side view	RLS	46 238	5.64	0.59	10	1	9
Foot angle	FA	46 238	4.92	0.71	14	1	8
Udder trait							
Fore udder attachment	FUA	46 238	6.55	0.90	14	1	9
Rear udder height	RUH	46 238	6.48	0.77	12	1	9
Rear udder width	RUW	46 238	5.65	1.09	19	1	9
Udder support	UC	46 238	6.20	0.84	13	1	9
Udder depth	UD	46 238	6.94	0.69	10	1	9
Front teat placement	FTP	46 238	4.69	0.85	18	1	9
Rear teat placement	RTP	14 061	5.34	0.95	18	1	9
Front teat length	FTL	22 482	4.32	0.98	23	1	9

CV = coefficient of variation; SD = standard deviation; Min = minimum; Max = maximum

The mean phenotypic scores for stature and chest width were 5.4 and 5.6, respectively, and close to the ideal score of 6. Mean score for body depth was approximately 7 (ideal score 6) and 6.6 (ideal score 8) for dairy strength, which indicate towards a deeper, but more frail cow. In terms of the structural body traits, rump angle, and rear legs side view, the scores were in the range of the respective ideal scores. The results on the structural body traits indicate, on average, a narrower, lower foot angled, and hocked rear leg cow. For udder traits, fore udder attachment and rear udder height were approximately 1.5 points lower than the ideal score of 8. A similar result was observed for rear udder width. Front teat placement was more than 2 points below the ideal score of 7, indicating on average a wider, more undesirable front teat placement. Scores for udder depth and udder cleft were close to the ideal scores of 7 and 6, respectively. Scores for rear teat placement and teat length were also close to the intermediate scores of 5.

Genetic correlations between functional herd life and conformation traits are presented in Table 5.3. Correlations between functional herd life and body structure traits were variable. In general, body structure traits had a low to moderate negative correlation with functional herd life (-0.04 to -0.27), except for stature where the genetic correlation was positive (0.15). Samoré *et al*. (2010), in a study on Italian Brown Swiss, also found low to moderate negative genetic correlations between body structure traits and functional herd life (-0.07 to -0.22). However, only body depth, dairy strength, rump angle, thurl width and rear legs side view were significantly correlated with functional herd life in the current study. The small genetic correlation between rear legs side view and functional herd life observed in the current study is consistent with the results by Vollema & Groen (1997) who reported a negative genetic correlation between rear legs side view and functional herd life (-0.17). Cassandro *et al*. (1999) reported a slightly higher negative genetic correlation between rear legs side view and functional herd life of -0.29 than in the current study. Cruickshank *et al*. (2002) and Tsuruta *et al*. (2005) reported a somewhat smaller genetic correlation between rear legs side view and functional herd life than in the current study. In the current study, rear legs side view is a trait with an intermediate optimum. Our results indicate that sickled cows will have a shorter functional herd life compared to straight legs cows. This is not consistent with the fact that rear legs side view is an intermediate optimum trait. In fact, Buenger *et al*. (2001) observed that sickled rear legs and extremely straight legs led to a lower functional length of productive life; a result that is in accordance with the curvilinear biological relationship between the two traits indicates that the statistical approach used may not be most appropriate. Therefore, the negative genetic correlation observed in the current study should be interpreted cautiously.

Although not significant, a moderate genetic correlation between dairy strength and functional herd life was observed in the current study. However, corresponding genetic correlations ranging from -0.29 to 0.47 were reported in literature (Short & Lawlor, 1992; Weigel *et al.*, 1998; Cruickshank *et al.*, 2002; Zavadilová *et al.*, 2009; Samoré *et al.,* 2010). For example, Cruickshank *et al.* (2002), in a study on registered US Guernsey cows, reported a moderately negative estimate of genetic correlation between dairy strength with functional herd life (-0.29).

The genetic correlation between body depth and functional herd life in the current study was small and negative (-0.19). Zavadilová *et al.* (2009) reported a similar negative genetic correlation (-0.16) in a study on Czech Fleckvieh cows. Weigel *et al.* (1998) and Samoré *et al.* (2010) found slightly lower genetic correlations of -0.07 and -0.10, respectively. Tsuruta *et al.* (2005) found a somewhat higher genetic correlation (-0.26) between body depth and functional herd life. The negative correlation between body depth and functional herd life indicates that cows with high scores for body depth (very deep) will tend to have a lower functional herd life. However, cows with low scores (shallow) will have longer functional herd life. This may present a problem for selection since it is known that body depth is an intermediate optimum trait.

Rump angle was negatively correlated (-0.19) with functional herd life in the first lactation in the current study. This genetic correlation was in agreement with the results (-0.11) reported by Cruickshank *et al.* (2002). However, the genetic correlation between rump angle and functional herd life reported in most of the studies ranged from 0.07 to 0.21 (Jairath *et al.*, 1998; Weigel *et al.*, 1998; Cruickshank *et al.*, 2002; Zavadilová *et al.*, 2009; Samoré *et al.,* 2010).

A moderate positive genetic correlation (0.33) was observed between foot angle and functional herd life in the third lactation in the current study. This positive genetic correlation indicates that foot angle is one of the most important potential indicators of functional herd life.

Smaller genetic correlations of 0.04 and 0.15 were reported by Cruickshank *et al*. (2002) and Tsuruta *et al*. (2005), respectively.

Significant moderate to high positive genetic correlations between most udder traits and functional herd life (0.23 to 0.63) were observed in the current study. Rear teat placement and front teat length were the only two udder traits that were not significant.

Table 5.3 Genetic correlations between functional herd life and conformation traits in the South African Jersey breed

Traits	**FHL1**	**FHL2**	**FHL3**
Body structure			
Stature	-0.04 ± 0.07	-0.05 ± 0.16	0.15 ± 0.13
Chest width	-0.04 ± 0.12	-0.14 ± 0.23	-0.15 ± 0.21
Body depth	-0.19 ± 0.10	-0.25 ± 0.21	-0.27 ± 0.10
Dairy strength	-0.01 ± 0.09	0.31 ± 0.17	0.29 ± 0.15
Rump angle	-0.19 ± 0.08	0.22 ± 0.15	0.15 ± 0.14
Thurl width	0.14 ± 0.10	-0.03 ± 0.13	-0.01 ± 0.17
Rear legs side view	-0.16 ± 0.06	-0.43 ± 0.21	-0.17 ± 0.17
Foot angle	0.16 ± 0.09	0.35 ± 0.19	0.33 ± 0.15
Udder traits			
Fore udder attachment	0.23 ± 0.10	0.63 ± 0.14	0.33 ± 0.15
Rear udder height	0.28 ± 0.09	0.54 ± 0.13	0.37 ± 0.14
Rear udder width	0.14 ± 0.08	0.36 ± 0.14	0.06 ± 0.13
Udder support	0.17 ± 0.09	0.36 ± 0.16	0.26 ± 0.15
Udder depth	0.10 ± 0.08	0.49 ± 0.18	0.39 ± 0.15
Front teat placement	0.08 ± 0.06	0.28 ± 0.13	0.19 ± 0.12
Rear teat placement	-0.03 ± 0.11	-0.21 ± 0.25	0.29 ± 0.18
Front teat length	0.10 ± 0.09	-0.34 ± 0.17	-0.07 ± 0.10

FHL1; FHL2; FHL3= functional herd life for lactation 1, 2 and 3 respectively.

It is important to note that the genetic correlations were more pronounced in the second lactation for all the udder traits, except for rear teat placement. These genetic correlations indicate that fore udder attachment, rear udder height, rear udder width, udder support, front teat placement and udder depth are the most useful indicators of functional herd life. Consistent with our genetic correlations between udder depth and functional herd life of 0.39 and 0.49, similar estimates ranging from 0.28 to 0.43 were reported in the literature (Vollema & Groen, 1997; Cassandro *et al*., 1999; Vukasinovic *et al*., 2002; Samoré *et al*., 2010). This general consistency across studies of the genetic correlation between udder depth and functional herd life indicates that udder depth is one of the most versatile indicators of functional herd life. Therefore udder depth should receive higher priority in the genetic evaluation for functional herd life.

The genetic correlation between udder support and functional herd life was 0.36 in the second lactation in the current study. In general, the corresponding estimates reported in the literature were variable ranging between -0.06 to 0.31 (Cassandro *et al*., 1999; Cruickshank *et al*., 2002; Vukasinovic *et al*., 2002; Tsuruta *et al*., 2005; Samoré *et al*., 2010).

Literature estimates for genetic correlation between fore udder attachment and functional herd life ranged from 0.15 to 0.32 (Cassandro *et al*., 1999; Vukasinovic *et al*., 2002; Tsuruta *et al*., 2005). While our corresponding estimates overlap with the literature estimates, our highest estimate (0.63) is almost double that of the highest reported value (0.32).

The genetic correlations between rear udder height, rear udder width and front teat placement with functional herd life found in the current study were generally higher than those reported in the literature. Our estimates ranged from 0.28 to 0.54 while the corresponding range for literature estimates was -0.07 to 0.21 (Cruickshank *et al*., 2002; Vukasinovic *et al*., 2002; Tsuruta *et al*., 2005). Buenger *et al*. (2001), Larroque & Ducrocq (2001), and Schneider *et al*. (2003) reported that cows with extremely close rear teats were more likely to be culled compared with cows with extremely wide rear teats.

5.4 Conclusions

Most of the body structure traits had a low to moderate negative genetic correlation with functional herd life in at least one lactation. All udder traits, except for rear teat placement and teat length, showed a significant positive genetic correlation with functional herd life. The following conformation traits were found to be useful indicators of functional herd life: udder depth, fore udder attachment, rear udder height, udder support, rear leg side view, foot angle and dairy strength. The genetic relationships between functional herd life and conformation traits in the South African Jersey breed indicate that conformation traits could be used to enhance the accuracy of genetic evaluation for functional herd life. It is therefore recommended that conformation traits should be included in the current national genetic evaluation for functional herd life in the South African Jersey breed.

Chapter 6

Assessment of inbreeding depression for functional herd life in the South African Jersey breed based on level and rate of inbreeding[4]

6.1 Introduction

Inbreeding will occur in any population of finite size unless specific measures are taken to avoid the mating of related individuals. Therefore, genetic improvement programmes should balance genetic gain with increases in inbreeding levels (Miglior *et al*., 1992). Increased inbreeding is usually considered undesirable because it leads to a decrease in genetic variation within a population, and in a reduction in performance in traits associated with the fitness (e.g. health, fertility, survival). While the impact of inbreeding in large populations is negligible, its effect in a typical livestock population where selective breeding is practiced cannot be ignored (Maiwashe *et al*., 2006). In practice, an increase in the coefficient of relationship among individuals results in increased difficulty in the selection of unrelated mates (Thompson *et al*., 2000a,b). It is furthermore important to maintain genetic diversity within a breed to ensure that future animals can respond to selection and changes in the environment. The net effect of inbreeding in a selection program will depend on the magnitude of the selection response relative to the possible depression and the rate of accumulation of inbreeding (Van Wyk *et al*., 2009).

Research shows that there is a general increase in the level of inbreeding in dairy cattle populations in different countries. In the Holstein population in United States, Young & Seykora (1996) obtained rates of inbreeding of 0.11% per year for the period 1960 to 1990. Thompson *et al*. (2000a) reported average rates of inbreeding of 0.04% during the 1970's, with an average

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[4] This chapter forms part of a peer-reviewed article published in the South African Journal of Animal Science. *S. Afr. J. Anim. Sci.* **42** (1), 55 – 62

yearly increase of 0.12% during the 1980's and continued to increase by 0.20% per year from 1990 to 1998 for the same population. The Canadian Dairy Network reported that the rate of inbreeding increased by 0.25% per year for the period 1990 to 2000 (http://www.cdn.ca).
Kearney *et al.* (2004) reported a rate of inbreeding of 0.03% per year from 1968 to 1991 and an increased rate of 0.17% per year for the period 1992 to 2002 in the United Kingdom Holstein population.

The detrimental impact of inbreeding on performance traits, especially those related to fitness, has been widely recognized and is a result of the reduction in heterozygosity as inbreeding accumulates (Falconer & Mackay, 1996). Inbreeding depression is a reduction of mean phenotypic values in animals that are inbred. If selection and inbreeding are applied simultaneously, deleterious alleles can possibly have their frequency diminished in the population (Norberg & Sorensen, 2007). The effect depends not only on the actual level of inbreeding, but also on the rate at which inbreeding is increasing. Van Wyk *et al.* (2009) suggested that slow inbreeding (1.53% per generation over 19 generations) allows natural selection to operate and to remove the less adapted animals; less inbreeding depression would then be expected among the individuals who accumulated the inbreeding over a larger number of generations for any given level of inbreeding. For example, animals with the same individual inbreeding coefficients could have different inbreeding depression effects due to differences in the number of generations in their own pedigree. González-Recio *et al.* (2007) developed an alternative method of fitting inbreeding coefficients accounting for the depth of known pedigree. This coefficient corrects the cumulative inbreeding coefficient regarding the pedigree depth of the individual and is an indicator of the increment in inbreeding regardless of the number of generations known in its pedigree (González-Recio *et al*., 2007).

While the detrimental effect of inbreeding on production traits in dairy cattle is well-documented, little information is available on the effect of inbreeding on longevity of cows (Thompson *et al*., 2000a; Caraviello *et al*., 2003; Sewalem *et al*., 2006). Smith *et al.* (1998) showed that an increase of one percent in inbreeding results in a decrease of 13.1 days of productive life. Cows in the Canadian population that are 10% inbred versus 5% had reduced longevity of 65 days (CDN, 2008). Rokouei *et al.* (2010) reported that cows with high levels of inbreeding were at higher relative risk of being culled. The objective of this study was to investigate inbreeding depression on functional herd life in the South African Jersey population based on individual level and rate of inbreeding.

6.2 Materials and Methods

A pedigree file of the South African Jersey breed (n = 903 759) was obtained from the Integrated Registration and Genetic Information System (INTERGIS). The data were checked for integrity (e.g. animals were ordered chronologically and no animals appeared as both a sire and dam) using the Animal Breeder's Tool Kit (ABTK: Golden *et al.*, 1992). The data included registered, grade and imported animals. Pedigree information of imported ancestors was retrieved from the INTERBULL database. These pedigrees were traced as far back as 1935. The percentages of animals in the pedigree file with 0, 1 or 2 parents known were 40%, 82% and 78%, respectively. The data used in this chapter is the same as the data used in chapter 3.

The inbreeding coefficient for each animal (F_i) in the pedigree was calculated using the *ainv* tool of the ABTK. The *ainv* tool implements the algorithm of Meuwissen & Luo (1992) to compute the inbreeding coefficients. Individual inbreeding coefficients were used to compute the individual rate of inbreeding (ΔF_i) according to the methodology described by Gonzalez-Recio *et al.* (2007) and modified by Gutiérrez *et al.* (2009). The ΔF_i is an alternative measure of inbreeding which is adjusted for the depth of known pedigree. Therefore, the individual rate of inbreeding makes it possible to distinguish between two animals with the same inbreeding coefficient, but different number of generations in which inbreeding was accumulated (González-Recio *et al.*, 2007; Gutiérrez *et al.*, 2009) . The individual rate of inbreeding was calculated as $\Delta F_i = 1- \sqrt[t-1]{1-F_i}$ where t is the number of known equivalent generations for the i^th^ individual. The t was calculated using the ENDOG v4.3 computer program (Gutiérrez & Goyache, 2005).

The effect of inbreeding on functional herd life in each of the first three lactations was estimated using a single trait sire model. The general form of the model fitted was as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zs} + \mathbf{e} \qquad [1]$$

where **y** is a vector of observations for productive herd life in each lactation, **b** is a vector of fixed effects of herd-year, registry status x herd size change x season of calving (rhs), age at calving (linear and quadratic), protein within rhs, protein and fat yield deviations (linear, quadratic and cubic), **s** is a vector of random sire effects, **e** is a vector of random residuals. The X and Z are incidence matrices relating fixed and random sire effects to observations, respectively. The random effects were assumed to be distributed as follows: $\mathbf{s} \sim N(\mathbf{0}, \mathbf{A}\sigma^2_s)$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma^2_e)$ where σ^2_s and σ^2_e are the sire and residual variances, respectively. The **A** and **I** are the numerator relationship and the identity matrices respectively. The sire and residual variances used in this study were calculated using heritability estimates reported by Du Toit *et al*. (2009).

Three analyses for functional herd life in each of the first three lactations were carried out using different variations of Equation 1. In the first analysis, an individual inbreeding coefficient (F_i) was fitted as a linear covariate in addition to the fixed and random effects in Equation 1. In the second analysis, the inbreeding coefficient was included as a discrete variable with the following classes of inbreeding: $0 < F \leq 3.125$, $3.125 < F \leq 6.25$, $6.25 < F \leq 12.5$ and $F > 12.5$ following the approach of Sewalem *et al.* (2006). In the third analysis, the individual rate of inbreeding (ΔF_i) was added to the model as a linear covariate. The individual rate of inbreeding was considered in the current study, because it automatically accounts for differences in pedigree depth.

The MTDFREML software package was used to estimate the effect of inbreeding on functional herd life and their corresponding approximate standard errors (Boldman *et al*., 1995).

6.3 Results and discussion

A summary of the data with details regarding the numbers of animals, mean level of inbreeding (%) by birth year cohort and the proportion of animals for each class of inbreeding, is shown in Table 6.1. In the 1985-1989 birth year cohort 71.0% of the population was not inbred, while only 15.6% of the animals were not inbred in the 2000-2003 cohort. There was a gradually increase in the level of inbreeding for the period 1985 to 1994, while the period 1995 to 2003 showed a rapid increase. The average level of inbreeding for the period 2000 to 2003 was 2.91%. This occurrence might be associated with superior sires being used more extensively, or possibly the incidence of more complete pedigree information.

Thompson *et al*. (2000a,b) reported average inbreeding coefficients of 4.2% and 4.6% for the American Holstein and Jersey populations, respectively. Sorensen *et al*. (2005) reported average inbreeding levels of 3.9% and 3.4% in 2003 in the Danish Holstein and Jersey breeds, respectively.

Table 6.1 Number of animals, mean level of inbreeding (%) by birth year cohort and percentage of animals in each class of inbreeding used in subsequent analyses

Birth year	No. of animals	Mean F (%)	Classes of inbreeding (%)					ΔF (% per year)
			F=0	0< F ≤3.125	3.125<F≤6.25	6.25<F≤12.5	F>12.5	
1985 - 1989	13 947	0.99	9 899 (71.0%)	2 399 (17.2%)	883 (6.3%)	498 (3.6%)	268 (1.9%)	0.327
1990 - 1994	31 753	1.19	14 153 (44.6%)	14 100 (44.4%)	2 122 (6.7%)	932 (2.9%)	446 (1.4%)	0.272
1995 - 1999	35 650	1.85	7 669 (21.5%)	21 041 (59.0%)	4 940 (13.9%)	1 599 (4.5%)	401 (1.1%)	0.343
2000 – 2003	8 910	2.91	1 386 (15.6%)	4 088 (45.9%)	2 455 (27.6%)	848 (9.5%)	133 (1.5%)	0.408

More recently, a slightly lower inbreeding level of 1.9% was reported for the Israeli Holstein population (Weller & Ezra, 2005). Among the five major breeds in Canada, all have an average inbreeding level between 5.50% (Ayrshire) and 6.64% (Guernsey) for registered animals born in 2009 (CDN, 2010). The Ayrshire and Jersey breeds have best controlled the rate of increase in the average inbreeding level since 2000, at -0.04% and +0.07% per year respectively, with the Holstein also at +0.08% per year. Similar results were obtained in a study by Maiwashe *et al*. (2006). The Jersey breed exhibited the highest annual rate of inbreeding (0.07%) followed by the Holstein (0.06%) and the Ayrshire and the Guernsey breeds, both with (0.05%). It should however be noted that differences in the levels of inbreeding in the different populations could be due to different base years. Figure 6.1 shows the mean annual inbreeding coefficients for Jersey animals born between 1939 and 2010. The average level of inbreeding for the Jersey breed is currently (2010) at 4.85% with a minimum and maximum of 0 and 31.34% respectively. The rapid increase in the level of inbreeding in the last 18 years is worth noting.

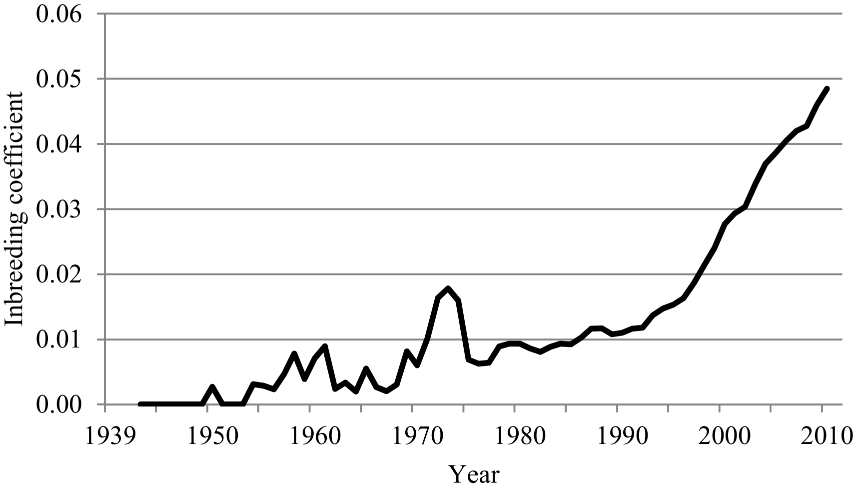

Figure 6.1 Mean annual individual inbreeding coefficients by birth year for the SA Jersey breed

The trend of the annual individual rate of inbreeding for SA Jersey animals born between 1940 and 2010, is presented in Figure 6.2. Noticeable is the sharp increase in the rate of inbreeding to approximately 0.92% per year in the early 1970's. According to Van Niekerk (personal communication) this incidence might be the result of suspension of importing semen during that period. In general, estimates of the rate of inbreeding obtained in this study are still lower than the critical level of 0.5% per year, suggested for animal breeding programs (Nicholas, 1989). However, estimates of the rate of inbreeding of the SA Jersey breed escalated since 2004 and are currently (year 2010) alarmingly high (0.55%).

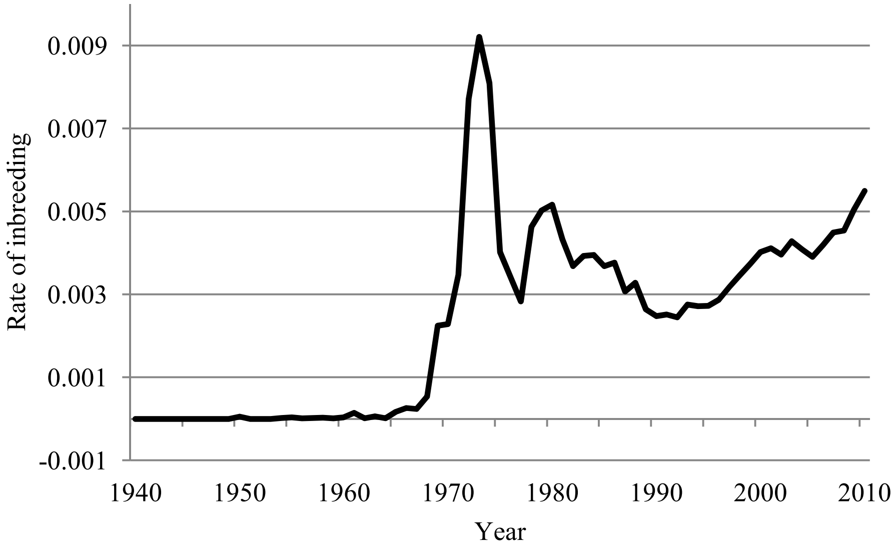

Figure 6.2 Mean annual individual increase in rate of inbreeding by birth year for the SA Jersey breed

The effect of inbreeding was expressed as a percentage of the mean to allow comparison with other similar studies. The results of the effect of inbreeding on functional herd life of the SA Jersey breed expressed as a percentage of the mean, are presented in Table 6.3. The mean survival in each lactation is also presented. The effect of inbreeding expressed as a percentage of the mean was -0.14% for the first lactation indicating that a one percent increase in inbreeding is associated with a reduction in mean survival of 0.14%. The current mean level of inbreeding (for the year 2010) in this study is 4.85%.

Based on this, the reduction in survival in the first lactation can be estimated to be 0.68%. The corresponding estimate for the second lactation is 1.70%. Miglior *et al.* (1992) also observed a significant reduction of -0.91% of the mean on productive life associated with a percentage increase in inbreeding in the Canadian Jersey population.

Table 6.2 Estimates of inbreeding depression (regression coefficients (b ± SE)) for functional herd life in the SA Jersey breed based on individual inbreeding coefficients (F_i) and rate of inbreeding (ΔF_i)

Lactation	b_{Fi} ± SE	P-value	$b_{\Delta Fi}$ ± SE	P-value
1	-0.0010 ± 0.0005**	0.0455	-0.1874 ± 0.1995	0.3472
2	-0.0025 ± 0.0007***	0.0004	-0.8975 ± 0.2723**	0.0010
3	-0.0015 ± 0.0010	0.1336	-0.5613 ± 0.3704	0.1285

** indicates significance at 5%, *** indicates significance at 1%.

Thompson *et al.* (2000a,b) reported a decline in survival as the level of inbreeding increases. Inconsistencies in the magnitude of estimates of the effect of inbreeding across studies could be due to the different rates and levels on inbreeding in different populations. For example, the level of inbreeding in the Canadian Jersey population in 2009 was higher than the current level of inbreeding in the South African Jersey populations (5.92% *vs* 4.85%).

The two measures of inbreeding (F_i and ΔF_i) used to estimate regression coefficients in the current analyses both detected a decline in functional herd life with increased inbreeding. Although the individual inbreeding coefficient is the most common parameter used in most inbreeding studies, it has a disadvantage that it cannot account for the depth of known pedigree. The rate of inbreeding (ΔF_i) is an alternative parameter that relates the increase of the individual inbreeding of animals in the population, accounting for the amount of known pedigree (González-Recio *et al*., 2007). This property is an advantage of ΔF_i over F_i when pedigree is incomplete. The higher level of inbreeding depression of functional herd life obtained when using ΔF_i in comparison with F_i (Table 6.2), is in accordance with results of González-Recio *et al*. (2007) in female fertility and calving ease in Spanish dairy cattle. From the results of a study with Spanish horses, Gómez *et al.* (2009) recommended the use of the individual increase in inbreeding coefficient (ΔF_i) instead of the individual inbreeding coefficient (F_i) due to the better fit with data and the special property whereby individual inbreeding coefficients are adjusted for the known pedigree depth.

Table 6.3 Mean survival (%), estimates of inbreeding depression (regression coefficients) for longevity in SA Jersey breed expressed as a percentage of the mean

Lactation	Mean survival (%)	b	% of the mean
1	73%	-0.0010	-0.14
2	72%	-0.0025	-0.35
3	67%	-0.0015	-0.22

The effect of inbreeding was also estimated considering inbreeding as a class variable. This analysis was conducted to gain better understanding of the dynamics of the effect of inbreeding as inbreeding increases. The results presented in Table 6.4 are in general agreement with the results from the regression analysis (Table 6.2). When inbreeding was treated as a class variable, animals with low inbreeding coefficients of between 0 and 3.125% were not significantly ($P > 0.05$) affected compared to non-inbred animals ($F_i = 0$).

Table 6.4 Estimates of the contrasts between inbreeding classes expressed as deviation from the non-inbred group (average $F_i = 0$) for the SA Jersey breed

Inbreeding Class (%)	Lactation ± SE		
	1	2	3
$0 < F \leq 3.125$	-0.0080	0.0001	-0.0104
$3.125 < F \leq 6.25$	-0.0110	-0.0135	0.0025
$6.25 < F \leq 12.5$	-0.0150	-0.0047	-0.0212
$F > 12.5$	-0.0250	-0.0366	-0.0095

However, as inbreeding increased from 3.125 to 6.25% and higher, a more pronounced decline in functional herd life was observed in all lactations. As shown in Table 6.4, a negative trend was observed as inbreeding increased in lactation 1. In contrast, no clear pattern was observed with lactations 2 and 3, respectively.

6.4 Conclusions

The effect of inbreeding on functional herd life was assessed for South African Jersey cattle using two measures of inbreeding. Significant negative effects of inbreeding on functional herd life were observed in the first and second lactation. However, no significant association was observed between inbreeding and functional herd life in the third lactation. The results from the current study indicate that the current levels of inbreeding or rate of inbreeding has reached levels that are detrimental to functional herd life. Therefore, individual inbreeding coefficients should be considered when breeding decisions are made by the Jersey breeders.

Chapter 7

General conclusions

Functional herd life is an economically important trait in dairy production because longer herd life is associated with lower heifer replacement costs and a higher proportion of productive mature cows in the herd. Our results indicate that approximately 25% of the cows survive until the third lactation. This high level of erosion in the Jersey breed is a course for concern. It is therefore important that sustainable interventions to remedy the situation are needed. In the current study we focussed on developing a selection tool for improving functional herd life. Successful implementation of a national genetic evaluation system for functional herd life requires development of the operational analytical model and subsequent estimation of genetic parameters.

A comprehensive operational model for genetic analysis of functional herd life, including important fixed and random effects, was developed. In the current study functional herd life was defined as survival in each of the first three lactations i.e. three genetically distinct measures of functional herd life. Genetic parameters estimated in this study suggest that sufficient genetic variation exist for functional herd life to allow for genetic improvement through selection. The moderate positive genetic correlation between survival in the first and third lactation suggest that early selection for functional herd life is feasible.

The operational model for functional herd life together with the genetic and residual (co)variance estimates obtained in the current study were used to develop a system for prediction of breeding values. Using this system a prototype breeding value for functional herd life was developed and successfully implemented in the national genetic evaluation system of the South African Jersey breed. The breeding value for functional herd life developed in this study provided Jersey breeders with a tool for direct selection for durable cows. In conjunction with breeding values for other traits (e.g. production, health and fertility) the breeding value for functional herd life should allow for more balance selection and breeding of Jersey cows. That is, apart from maintaining high levels of production, Jersey breeders should be able to breed a more durable cow. While the new selection tool developed in the current study will allow for direct selection for functional herd life, the genetic response from selection could be relatively slow due to the low heritability and long generation interval. The challenges associated with direct selection for functional herd life provides opportunities for looking at other alternatives to enhance the accuracy of genetic evaluation for functional herd life. Correlated conformation traits could provide such an alternative.

Genetic correlations between conformation traits and functional herd life were estimated in the current study to investigate the utility of conformation traits as early indicators of functional herd life. For ease of presentation, conformation traits were categorized into body structure and udder traits. Our results show that most of the body structure traits had low to moderate negative genetic correlations with functional herd life. All udder traits, except for rear teat placement and teat length, showed a significant positive genetic correlation with functional herd life. The following conformation traits were found to be useful indicators of functional herd life: udder depth, fore udder attachment, rear udder height, udder support, rear leg side view, foot angle and dairy strength. Our results indicate that conformation traits could be used to enhance the accuracy of genetic evaluation for functional herd life.

Some of the conformation traits exhibit an intermediate optimum. The relationship between these traits and functional herd life is nonlinear or curvilinear. In the current study we estimated linear genetic correlations between conformation traits and functional herd life. This is despite the fact that the relationships could be curvilinear. If the relationship between conformation traits and functional herd life is strongly curvilinear then the linear correlations estimated in the current study may be inadequate in describing the relationship between conformation traits and functional herd life. Use of linear genetic correlations to study the relationship between functional herd life and conformation traits is a common practice in animal breeding research.

The effect of inbreeding on functional herd life was assessed for South African Jersey cattle using two measures of inbreeding. Significant inbreeding depression on functional herd life was observed in the first and second lactation. The results from the current study indicate that the current levels or rate of inbreeding have reached levels that are detrimental to functional herd life.

The results from the current research present a number of opportunities. Firstly, the framework developed here can be easily adapted for application in other dairy breeds. Secondly, the results from this study could provide baseline information for calculation of relative economic values for functional herd life.

Recommendations from the current study are as follows:

- The prototype breeding value for functional herd life developed in the current study should first be validated using Interbull Trend Validation Tests 2 and 3 before implementation in the national genetic evaluation for the Jersey breed.
- Conformation traits should be included in the current national genetic evaluation for functional herd life in the South African Jersey breed.
- Further research should be conducted to gain better understanding of the repercussions of applying linear genetic correlations in describing the relationship between conformation traits and functional herd life.
- Individual inbreeding coefficient should be considered when breeding decisions are made by the Jersey breeders.

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