Estimates of genetic parameters for female fertility traits from a dairy selection experiment for fat plus protein by using random regression and linear-threshold animal models

by

Gustavo Augusto Gutierrez

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

Major: Animal Breeding and Genetics (Quantitative Genetics)
Program of Study Committee:
P. Jeffrey Berger, Major Professor
Jack C. Dekkers
Philip L. Spike
Steven M. Hopkins
Curtis R. Youngs
Max D. Morris

Iowa State University

Ames, Iowa

2010

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS

AI: Average information algorithm

AM: Animal model

AFP: Average PTA for fat plus protein

CS-B: Binary calving success

CS-B$_x$: Binary calving success at parity "x"

CS-T: Three-category calving success

CS-T$_x$: Three-category calving success at parity "x"

CF: Covariance function

CONL: Interval from conception to date leaving herd

CS: Calving success

DO: Days open

DPR: Daughter pregnancy rate

EF: Eigenfunction

FBL: Interval first breeding to date leaving herd

FLS: Functional lactation survival

FPE: Fraction of permanent environmental effect

GS: Gibbs sampling

HFP: High PTA for fat plus protein

ISU: Iowa State University

ML: Maximum likelihood

MT: Multiple trait

MTSM: Multiple trait sire model

NEB: Negative energy balance

NR: Not reported

PCL: Interval from last calving to date leaving herd

PTA: Predicted transmitting ability

RAM/REP: Repeatability animal model.

 REML: Restricted maximum likelihood

REMLT: Restricted maximum likelihood type procedure

RR: Random regression model

SM: Sire model

ST: Single trait

STY: Stayability

TT: Two trait

TSM: Threshold sire model

TLAM: Threshold-linear analysis with animal model

USA: United States of America

UK: United of Kingdom

ABSTRACT

The main objective was to evaluate different models to improve the genetic analysis of days open (DO) in dairy cattle. Thus, three studies were conducted: 1) to evaluate the use of a linear random regression model for DO; 2) to study the genetic variation of calving success (CS); and 3) to evaluate the joint analysis of DO and CS by a threshold linear animal model.

The objective of the first study was to investigate the feasibility of using a linear Legendre random regression model for the analysis of female fertility as expressed by DO. The analysis provided insight about the kind and amount of variation over the trajectory for age at calving from 24 to 90 mo. An aging and genetic component of female fertility was discovered. Heritability ranged from 0.07 to 0.10 from 24 to 72 mo. Permanent environmental correlations between fixed ages at calving changed from positive to negative values with greater distance between days open in young cows and days open in older cows; $r(24,36) = 0.88$, $r(24,72) = -0.65$. The random regression animal model is a better alternative to a repeatability animal model for estimation of variance components of DO. However, the assumption of genetic correlation of unity between adjacent parities is not realistic. Further research is needed to evaluate the advantages of using random regression model on the genetic analysis of DO.

The objective of the second study was to investigate genetic parameters for calving success (CS) at different parity groups. Three definitions of CS were evaluated: CS-B had two categories (1=success and 2=failure), CS-T (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve), and CS-T2 (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve). Data from 1236 Holstein females from parity 0 to 5 were analyzed with threshold animal model. Posterior means of

heritability for CS-B from parity 0 to 5 were slightly lower than those for CS-T. Posterior means of heritability for CS-B were 0.16(.08), 0.08(.03), 0.23(.07), 0.23(0.07), 0.24(.08) and 0.17(.08) for parity 0 to 5, respectively. Posterior means of heritability for CS-T were 0.17(.08), 0.10(.03), 0.21(.06), 0.22(0.07), 0.28(.08) and 0.21(.08) for parity 0 to 5, respectively. Posterior means of heritability for CS-T2 were 0.10(.07), 0.09(.04), 0.29(.06), 0.27(0.08), 0.24(.08) and 0.30(.09) for parity 0 to 5, respectively. Posterior means of genetic correlations between adjacent calving opportunities for CS-B, CS-T, and CS-T2 were variable in sign and magnitude with high posterior standard deviations. Our results indicate that CS-B, CS-T, and CS-T2 have substantial genetic variation to allow genetic improvement of female fertility. Some advantages of using CS for genetic evaluation of sires for female fertility is that it includes fertility performance of both heifer and lactating cows and it takes into account censored records for days open.

The objective of the third study was to investigate genetic parameters for both DO and CS at different parity groups. The joint analysis of DO with CS-B, CS-T, and CS-T2 were done by a linear-threshold animal model. Data from 1236 Holstein females from parity 0 to 4 were used. Posterior means of heritability for CS-B, CS-T, and CS-T2 were low to moderate. Posterior means of heritability for CS-B from parity 0 to 4 were similar than those for CS-T and CS-T2. Posterior means of CS-B heritability were 0.14(.04), 0.09(.03), 0.28(.07), 0.25(0.06), and 0.26(.06) for parity 0 to 4, respectively, CS-T heritability posterior means were 0.13(.04), 0.09(.03), 0.26(.06), 0.24(0.06), and 0.28(.06) for parity 0 to 4, respectively, and CS-T2 heritability posterior means were 0.15(.04), 0.09(.03), 0.28(.06), 0.26(0.06), and 0.26(.06) for parity 0 to 4, respectively. Posterior means of heritability for DO from joint analysis with CS-B, CS-T and CS-T2 were similar, and they increased from low to moderate

with parity. Posterior means of genetic correlations between DO and CS in the same parity were positive and varied from low to moderate, but they had large posterior standard deviations. CS is a categorical trait with similar genetic variation as DO and it is analyzed jointly with DO to make effective use of the genetic correlation between these two traits in lactating cows. The joint analysis can identify cows with greater genetic merit for conception at an earlier stage of lactation and greater success at maintenance of pregnancy.

Key words: Days open, calving success, random regression, female fertility.

CHAPTER 1. GENERAL INTRODUCTION

INTRODUCTION

Genetic progress for milk yield has increased since 1960 due to the higher selection intensity for sires and higher reliability of sire's Predicted Transmitting Ability (PTA) from modern progeny testing schemes (Powell and Norman, 2006). Female fertility, however, has deteriorated in Holsteins (Abdallah and McDaniel, 2000; Lucy, 2001). An increasing genetic trend for days open was observed in Holstein cows from North Carolina experimental herds (Abdallah and McDaniel, 2000) and a declining genetic trend for pregnancy rate was reported from cows born from 1960 to 1995 for most dairy cattle breeds in US (Van Raden et al., 2004).

Female fertility is of significant economic importance to dairy producers. Poor female fertility performance restricts the rate of genetic gain for milk yield, increases insemination costs, leads to premature culling, and reduces the overall milk yield per cow (Norman et al., 2009). The marginal cost for additional days open varies from $ 0.81 to $13.3 and increases with longer days to conceive (De Vries et al., 2004). Therefore, selection for female fertility will lead to reduced costs at farm level and increased longevity in dairy cattle.

Days open (DO) is the most common trait used for genetic evaluation for female fertility in dairy cattle, because it is easy to record at dairy farms (Gonzales-Recio et al., 2006). In addition, a linear transformation of DO has been used for predicting breeding values of daughter pregnancy rate (DPR) in US (Van Raden et al., 2004). The repeatability model is the current statistical method used for genetic evaluation of DO. The main assumption of this model is that genetic correlation between adjacent parity groups is equal to one and that

environmental correlations are similar among parity groups. Such assumptions may not have a biological basis for fertility traits, therefore appropriate model must be found for analysis of repeated records for DO.

Because a cow could have repeated days open (DO) records in her lifetime, DO can be analyzed as a function valued-trait (Meyer and Kirkpatrick, 2005) by using a Legendre polynomial random regression model (Schaeffer, 2004). The use of random regression model (RRM) allows one to study changes in genetic and permanent environmental variances throughout the age at calving trajectory and the prediction of breeding value profiles for each animal.

An unbiased genetic analysis of DO may include fertility records from cows that did not calve in a subsequent parity (Van Raden, personal communication, 2004). Exclusion of records of cows that did not conceive or calve again from data sets would lead to bias in genetic evaluation (Marti and Funk, 2004). The bias will result as reproductive data sets may contain information from either fertile cows or high milk yielders or both (Kadarmideen et al., 2003). In a bivariate analysis of DO for parity 1 and 2, the removal of cows that had no opportunity for a second parity increased sire variance estimate for DO at first parity but not for DO at second parity (Jansen et al., 1987).

A bivariate linear-threshold approach was used to account for censored data in the analysis of a reproductive trait in beef cattle (Urioste et al., 2007b) and dairy cattle (Hou et al., 2009). Application of this approach assumes that one trait follows an underlying continuous distribution and that it can be analyzed by using a linear model e.g., calving date, and that it is censored by a correlated categorical trait (e.g. calving success: 1=success; and 2=failure). This approach was applied by Arnason (1999) for genetic evaluation of racing

horses and it was described by Foulley (2004) for mixed model analysis under stochastic censoring. The idea of using a similar two-trait analysis to account for conception and maintenance of pregnancy as being suitable for use in the analysis of fertility traits in dairy cattle was proposed by using a joint analysis of calving success and days open (Misztal, personal communication, 2007; Huang et al., 2007).

The objective of this dissertation is to estimate heritability and genetic correlation for days open by using two statistical approaches such as a linear random regression for age at calving and a linear-threshold analysis between days open and calving success.

DISSERTATION ORGANIZATION

The dissertation is comprised of 5 chapters. The first chapter contains a general introduction and review of literature for the whole dissertation. Chapters two to four are written as a separated papers that each focus on a particular aspect of the estimation of genetic parameters for days open and calving success. Chapter two provides a comparison among multiple trait model, random regression model, and repeatability model for variance component estimation of days open. Chapter three gives the genetic analysis of calving success as a binary or three-category trait by using a set of multiple-trait threshold animal models. Chapter four, following the results for chapter three, gives the joint genetic analysis of days open and calving success by using a set of multiple-trait linear-threshold animal models. Chapter five gives the general conclusions from the previous three chapters.

LITERATURE REVIEW

Days open

Female fertility of lactating cows is a very complex trait, it can be defined as the cow's ability to a) resume ovary function after calving, b) show a detectable estrus, c) become pregnant and d) maintain pregnancy and succeed at calving. Therefore, many traits have been used as indicators of female fertility performance, e.g., days open (DO) (Dematawewa and Berger, 1998; Oseni et al., 2004; Gonzalez-Recio et al., 2006; Huang et al., 2007), number of services (Chang et al., 2006), or non-return rate (Heringstad et al., 2006).

Days open is defined as the interval from calving to conception in dairy cattle. It is a compound trait affected by factors affecting the cow's ability to resume ovary function after calving, to show a detectable estrus, and to become pregnant. Also, DO records in a herd are characterized by having repeated measurements per cow and for being highly unbalanced due to death or involuntary culling for reasons such as reproductive failure, severe mastitis, etc. (Dematawewa and Berger, 1998; Oseni et al., 2004; Gonzalez-Recio et al., 2006; Huang et al., 2007).

Furthermore, DO is easy to measure from dairy recording data at the farm level and it was the choice for female fertility genetic evaluation in the United States. Since 2004, a linear transformation of DO has been used for predicting breeding values of daughter pregnancy rate (Van Raden et al., 2004). The repeatability model is the current statistical method used for genetic evaluation of DO. The main assumption of this model is that the genetic correlation between adjacent parity groups is equal to one and that environmental correlations are similar among consecutive parity groups. Such assumptions may not have a

biological basis for fertility traits, therefore an appropriate model must be found for analysis of repeated records for DO.

However, DO is strongly affected by environmental factors rather than genetic factors. Among environmental factors affecting DO are managerial decisions (voluntary waiting period), health, nutrition, welfare and management practices (heat detection and proper artificial insemination). Nevertheless, substantial genetic variability was detected to justify selection for DO in dairy herds (Philipsson, 1981).

Dematawewa (1996) reviewed heritability estimates for DO from studies done before 1996. Heritability estimates for DO have been very low regardless of data size, models or variance component estimation procedure. Table 1 shows heritability and repeatability estimates for DO from published studies. Heritability estimates for DO from field data by using repeatability animal model and similar editing criteria were about 0.04 (Dematawewa and Berger, 1998; Van Raden et al., 2004; Gonzales-Recio and Alenda, 2005). In contrast, a heritability estimate from experimental data for DO at Langhill (Scotland) was 0.13 using a repeatability animal model (Pryce et al., 1999).

In addition, variance component estimates for DO are highly influenced by the voluntary waiting period practices at farm level and editing procedures set by researchers (Oseni et al., 2004). The farm manager may delay insemination date in early lactation when the cow had high milk yield or heat stress in summer, thus longer DO were recorded due to longer voluntary waiting period. As a result some cows had longer DO due the management practices, this data would tend to bias variance component estimates (Van Raden et al., 2004; Oseni et al., 2004). Besides, the setting of upper limit for DO varied among studies, for instance the heritability estimate for DO increased 30% when the upper limit was changed

from 150 to 250 d, and both the genetic and residual variance increased as the upper limit

increased from 150 to 365 d (Oseni et al., 2004). To our knowledge nobody has reported

heritability estimates of DO using random regression models.

Table 1. Estimates of heritability (h^2) and repeatability (c^2) for days open reported in
published articles.

Source	Parity	Number of Records	h^2	c^2	Estimation Procedure
Hayes et al. (1992)	All	235,589	0.05	0.10	SM-REML
Marti and Funk (1994)	1 to 5	611,680	0.05	0.14	SM-REML
Dematawewa and Berger (1998)	All	122,715	0.04	0.12	RAM-REML
Pryce et al. (1999)	All	2,506	0.13	0.33	RAM-REML
Abdallah and McDaniel (2000)	1 to 6	23,052	0.03	0.07	RAM-REML
Kadarmideen et al. (2003)	1 to 5	62,443	0.02	0.05	MT-RAM-REML
Van Raden et al. (2004)	1 to 5	2,195,643	0.04	0.13	RAM-REML
Gonzales-Recio and Alenda (2005)	All	113,375	0.04	NR	TT-RAM-REML

SM-REML: Single trait sire model and Restricted maximum likelihood, RAM-REML: Repeatability animal model and Restricted maximum likelihood; TT-RAM-REML: Two trait repeatability animal model and Restricted maximum likelihood, MT-RAM-REML: Multiple trait animale model and Restricted maximum likelihood. NR= Not reported.

Repeatability estimates for DO were low; therefore poor/bad fertility performance in a

given lactation may not be repeatable in subsequent lactations (Hansen et al., 1983a).

Repeatability estimates for DO from field data varied from 0.5 to 0.16 (Hansen et al., 1983a;

Dematawewa and Berger, 1998; Van Raden et al., 2004). Besides, the fraction of phenotypic

variance attributed to permanent environmental effect for DO ranged from 0.08 to 0.13

(Hansen et al., 1983a; Dematawewa and Berger, 1998; Van Raden et al., 2004).

Heritability estimates for DO in different parities and genetic correlations for DO

between adjacent parities are scarce in the literature, maybe due to the difficulty in

implementing a multiple trait analysis for DO (Jansen et al., 1987). Table 2 shows heritability

estimates and genetic correlation for DO at different parities. Heritability estimates for DO

tended to slightly increase with parity (Berger et al., 1981; Jansen et al., 1987; Raheja et al.,

1989). In one study genetic correlations between DO in different lactations were positive and

ranged from moderate to high (Jansen et al., 1987). Conversely, in another study genetic

correlations for DO in different parities were positive and close to zero (Raheja et al., 1989).

Table 2. Heritability estimates for days open in different parities.

Source	Parity	Number of Records	Heritability	Estimation Procedure
Berger et al. (1981)	1	17,112	0.02	ST-SM-Henderson III
	2	15,528	0.03	
	≥3	30,452	0.05	
Hansen et al. (1983a,b)	1	47,710	0.02	ST-SM-Henderson III
	2	31,162	0.03	
	3	22,389	0.03	
Jansen et al. (1987)	1	12,051-12,145	0.03	TT-SM-REML
	2	6,307-9,640	0.02	
	3	2,796-4,985	0.07	
Raheja et al. (1989)	1	46,322	0.03	MT-SM-ML
	2	12,007	0.04	
	3	1821	0.05	

ST-SM-Henderson III: Single trait sire model and Henderson III method, TT-SM-REML: Two trait sire model and Restricted maximum likelihood, MT-SM-ML: Multiple trait sire model and maximum likelihood.

Positive to moderate genetic correlation estimates between days open and either milk,

protein, or fat yield have been reported by many authors from studies using field data (Berger

et al., 1981; Hansen et al., 1983b; Nebel and McGilliard, 1993; Dematawewa and Berger,

1998, Abdallah and McDaniel, 2000, Kadarmideen et al., 2003; Van Raden et al., 2004). It

may be an indication of an antagonistic relationship between female fertility and yield traits

in dairy cattle. However, high yielding cows will show appropriate performance for fertility

if the appropriate environment is provided by the dairyman (Marti and Funk, 1994; Nebel and McGilliard, 1993; Lucy, 2001).

Random regression models

Random regression models (RR) have been applied in the analysis of repeated measurement data where the trajectory of time was either days in milk, age or parity (e.g., daily milk yield, Bohmanova et al., 2008; beef growth rate, Arango et al., 2004; lamb growth, Fischer et al., 2004; number of services, Nishida et al., 2006). RR modeling enables researchers to estimate mathematical functions (formally called covariance function (CF)) of the (co)variance between all possible points on the trajectory of time when each measurement is taken (Van der Werf, 2001). The CF is estimated from the (co)variance matrix of the RR coefficients (Meyer and Hill, 1997).

Schaeffer (2004), and Meyer and Kirkpatrick (2005) described the basic structure of RRM. Following is the basic structure as described by Schaeffer (2004):

$Y_{ijkn:t} = F_i + g(t)_j + r\,(a,x,m1)_k + r\,(pe,x,m2)_k + e_{ijkn:t}$, where:

$Y_{ijkn:t}$ is the nth observation on the kth animal at time t belonging to the ith fixed effect factor and the jth group, F_i is a fixed effect independent of the time scale, $g(t)_j$ is a function or functions that account for the phenotypic trajectory of the average observations across all animals belonging to the jth group; $r\,(a,x,m1)_k$ is the notation adopted for a random regression function for the additive genetic effects; $r\,(a,x,m1)_k = \sum_{l=0}^{m1} a_{kl}\,x_{ijk:l}$; $r(pe,x,m2)_k$ is the notation adopted for a random regression function for the permanent environment;

$r\,(pe,x,m2)_k = \sum_{l=0}^{m2} p_{kl}\,x_{ijk:l}$; a is the additive genetic effect of the kth animal; x is the vector of

time covariates; pe is the notation adopted for a random regression function; m1 is the order of the regression function for the additive genetic effects; m2 is the order of the regression function for the permanent environment; and $e_{ijkn:t}$ is a random residual effect.

Schaeffer (2004) stated that the function $g(t)_j$, can be either linear or nonlinear in time. Such a function is necessary in a RRM to account for the phenotypic relationship between the response variable and the time covariates. The random regression coefficients are intended to model the deviation around the phenotypic trajectories. The pattern of variation may be very different in shape or appearance from the phenotypic relationships, and maybe more simple than $g(t)_j$ (Schaeffer, 2004).

The eigenvalues and their corresponding eigenfunctions of the covariance matrix of the genetic additive random regression coefficients were used to indicate the pattern of genetic variation at all covariate values (Van der Werf, 2001). The magnitude of the eigenvalue relative to the trace of the CF coefficient matrix indicates the amount of variation that is explained by factors associated with each eigenvalue. A large eigenvalue indicates that the change caused by selection of the associated eigenfunction will happen faster. Thus, the trend of eigenfunctions is an indication of how the factors associated with each eigenvalue affects the pattern of variation at all covariate values (Meyer and Kirkpatrick, 2005).

Calving Success

Calving success (CS) is a compound trait that indicates cow's ability to conceive, to maintain pregnancy and to succeed at calving. CS has been used as a measure of female fertility in beef cattle (Meyer et al., 1990; Johnston and Bunter, 1996; Mercandante et al.,

2003; Donoghue et al., 2004; Urioste et al., 2007a,b). CS records were coded as 0 if the cow had not calved, as 1 if the cow succeed at calving at given parity (Urioste et al., 2007a,b).

Table 3 shows heritability estimates or posterior means for CS in different beef cattle breeds. Some researchers reported moderate heritability for CS (Urioste et al., 2007a,b; and Rust and Groeneveld, 2002) whereas others reported low heritability for CS (Meyer et al., 1990; Johnston and Bunter, 1996; Mercandante et al., 2003; Donoghue et al., 2004; Van der Westhuizen et al., 2001).

To the best of my knowledge, CS has not been investigated in dairy cattle as a female fertility trait. However, some researchers have investigated the use of CS as a correlated variable with DO in order to account for censored data of DO in Holstein by using simulation (Huang et al., 2007). A linear-threshold model of DO with upper limit of 250 days and CS was more accurate in sire variance and heritability estimates (Huang et al., 2007).

Few studies have reported genetic correlations between CS records from different parities in beef cattle (Urioste, 2007a,b).   In one study genetic correlations were moderate to high, but highly variable, and genetic correlations for adjacent parities were negative (Urioste, et al., 2007a). In another study genetic correlations between CS from different parities were positive (Urioste, et al., 2007b).

On the other hand, traits like longevity in dairy cattle as stayability (Van Vleck, 1980; Van Doormaal et al., 1985) and functional lactation survival (Jairath et al., 1998) are based on survival status within a cow's lifetime to a fixed endpoint. Stayability (STY) is the survival status at certain fixed ages, eg. 36, 48, 60, 72 and 84 months of total life (Van Vleck, 1980; Hudson and Van Vleck, 1981) or 17, 30, 43, and 55 mo of productive life (Van Doormaal et al., 1985), whereas functional lactation survival (FLS) is the survival status at

given lactation eg. first, second, and third lactation (Jairath et al., 1998). Both STY and FLS are defined as a binary trait (1=if cow survived to the specific time, 0=if cow did not survived). Also, CS can be viewed as an indirect measure of survival, because cows which did not calved at a given parity were culled. However, CS may not be the same trait as STY or FLS in dairy cattle.

Table 3. Heritability estimates (standard error) or posterior means (posterior standard deviation), and statistical procedure for calving success in beef cattle.

Source	Breed	Parity	Number of Records	Scale	Heritability	Statistical procedure
Urioste et al. (2007a)	Angus	1	2032	Liability	$0.30(0.10)^2$	MT-TSMGSM-GS
		2	1080		$0.35(0.17)^2$	
		3	947		$0.27(0.14)^2$	
Urioste et al. (2007b)	Angus	1	6763	Liability	$0.42(0.06)^2$	MT-TLAM-GS
		2			$0.40(0.05)^2$	
		3			$0.37(0.14)^2$	
Donoghue et al.(2004)	Angus	1	16358	Liability	$0.03(0.01)^2$	TL-AM-B
Mercandante et al. (2003)	Nellore	1	926	Liability	$0.04(0.06)^1$	TAM-REML
		2	601		$0.10(0.07)^1$	
Van der Westhuizen et al. (2001)	Multibreed composite	0 to 4	26177	Liability	0.03^1	TSM-REMLT
Rust and Groeneveld (2002)	Afrikaner	All	3922	Liability	0.27^1	TSM-REMLT
Johnston and Bunter (1996)	Angus	0	5670	Observed	0.11^1	AM-REML
Meyer et al. (1990)	Hereford	All	2685	Observed	0.08^1	RAM-REML
	Angus		4282		0.02^1	
	Zebu cross		3105		0.08^1	

1: Heritability estimates, 2: Heritability posterior means, MT-TSMGSM-GS: Multiple trait threshold sire-maternal grand sire model and Gibbs sampling, MT-TLAM-GS: Multiple trait threshold-linear animal model and Gibbs sampling, TL-AM-B: Threshold linear analysis with animal model and Bayesian analysis. TAM: Threshold animal model; AM: Animal model; REML: Restricted maximum likelihood, TSM-REMLT: Threshold sire model and REML type procedure, and RAM: Repeatability animal model.

Both STY and FLS have low heritability estimates reported in the literature. Heritability estimates for STY at 17, 30, 43, and 55 mo of productive life ranged from 0.01 to, 0.04 (Van Doormaal et al., 1985), and heritability estimates for STY at 42, 54, 66 and 78 mo of total life ranged from 0.04 to 0.06, and for STY at 36, 48, 60, 72, and 84 mo of total life ranged from 0.02 to 0.05 (Hudson and Van Vleck, 1981). Heritability estimates for FLS were 0.03 at lactation 1, 2 and 3 (Jairath et al., 1998). The latter estimates were obtained ignoring the categorical nature of STY and FLS.

Genetic correlations among productive life traits for STY were very high, but genetic correlations among total life traits for STY were lower and variable (Van Doormaal et al, 1985). Genetic correlations between STY to different ages ranged from 0.71 to 1.00 (Hudson and Van Vleck, 1981). Genetic correlations for FLS were 0.62, 0.57 and 0.75 between lactation 1 and 2, 1 and 3, 2 and 3, respectively (Jairath et al., 1998).

REFERENCES

Abdallah, J. M., and T. B. McDaniel. 2000. Genetic parameters and trends of milk, fat, days open, and body weight after calving in North Carolina experimental herds. J. Dairy Sci. 83:1364-1370.

Arango, J. A., L. V. Cundiff, and L. D. Van Vleck. 2004. Covariance functions and random regression models for cow weight in beef cattle. J. Anim. Sci. 82:54-67.

Arnason, T. 1999. Genetic evaluation of Swedish standard-bred trotters for racing performance traits and racing status. J. Anim. Breed. Genet. 116:387-398.

Berger, P. J., R. D. Shanks, A. E. Freeman and R.C. Laben. 1981. Genetics aspects of milk yield and reproductive performance. J. Dairy Sci. 64:114-122.

Bohmanova, J., F. Miglior, J. Jamrozik, I. Misztal, and P.G. Sullivan. 2008. Comparison of random regression models with Legendre polynomials and linear splines for production traits and somatic cell score of Canadian Holstein cows. J. Dairy Sci. 91:3627-3638.

Chang, Y. M., I. M. Andersen-Ranberg, B. Heringstad, D. Gianola, and G. Klemetsdal. 2006. Bivariate analysis of number of services to conception and days open in Norwegian Red using a censored threshold-linear model. J. Dairy Sci. 89:772-778.

Dematawewa, C. M. B. 1996. Economic analysis of alternative breeding programs. Ph. D. dissertation. Iowa State University, USA.

Dematawewa, C. M. B., and P. J. Berger. 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins. J. Dairy Sci. 81:2700–2709.

De Vries, A.J. VanLeeuven, and W. Thatcher. 2004. Economic importance of improved reproductive performance. In proceedings 2004 Florida Dairy Reproduction Road Show. pp 33-43.

Donaghue, K. A., R. Rekaya, J. K. Bertrand, and I. Misztal. 2004. Threshold linear analysis of measures of fertility in artificial insemination data and days to calving in beef cattle. J. Anim. Sci. 82:987-993.

Fischer, T. M., J. Van der Werf, R. G. Banks, and A. J. Ball. 2004. Description of lamb growth using random regression on field data. Livest. Prod. Sci. 89:175-185.

Foulley, J. L. 2004. Prediction of random effects in linear mixed models under stochastic censoring. Proc. of stat. in Health Sciences. June 2004, 23-25. Nantes, France.

González-Recio, O. and R. Alenda. 2005. Genetic parameters for female fertility traits and fertility index in Spanish dairy cattle. J. Dairy Sci. 88:3282-3289.

González-Recio, O.Y., M. Chang, D. Gianola, and K. A. Weigel. 2006. Comparison of models using different censoring scenarios for days open in Spanish Holstein cows. Anim. Sci. 82:233-239.

Hansen, L. B., A. E. Freeman, and P. J. Berger. 1983a. Variances, repeatabilities, and age adjustments of yield and fertility in dairy cattle. J. Dairy Sci. 66:281-292.

Hansen, L. B., A. E. Freeman, and P. J. Berger. 1983b. Yield and fertility relationships in dairy cattle. J. Dairy Sci. 66:293-305.

Hayes, J. F., R. I. Cue, and H. G. Monardes. 1992. Estimates of repeatability of reproductive measures in Canadian Holsteins. J. Dairy Sci. 75:1701-1706.

Heringstad, B., I. M. Andersen-Ranberg, Y. M. Chang, and D. Gianola. 2006. Short Communication: Genetic analysis of non-return rate and mastitis in first-lactation Norwegian Red cows. J. Dairy Sci. 89:4420-4423.

Hou, Y. P. Madsen, R. Labouriau, Y. Zhang, M. S. Lund, and G. Su. 2009. Genetic analysis of days from calving to first insemination and days open in Danish Holsteins using different models and censoring scenarios. J. Dairy Sci. 92:1229-1239.

Huang, C., I. Misztal, S. Tsuruta, and T. J. Lawlor. 2007. Methodology of evaluation for female fertility. Interbull Bulletin 37:156-159.

Hudson, G. F. S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64:2246-2250.

Jairath, L., J. C. M. Dekkers, L. R. Schaeffer, Z. Liu, E. B. Burnside, and B. Kolstad, 1998. Genetic evaluation for herd life in Canada. J. Dairy Sci. 81:550-562.

Jansen, J., J. Van der Werf, and W. de Boer. 1987. Genetic relationships between fertility traits for dairy cows in different parities. Livest. Prod. Sci. 17:337-349.

Johnston, D. J. and K. L. Bunter. 1996. Days to calving in Angus cattle: Genetics and environmental effects, and covariances with other traits. Livest. Prod. Sci. 45:13-22.

Kadarmideen, H., R. Thompson, M. Coffey, and M. Kossaibati. 2003. Genetic parameters and evaluations from single- and multiple-trait analysis of dairy cow fertility and milk production. Livest. Prod. Sci. 81:183-195.

Lucy, M. C. 2001. Reproductive loss in high-producing dairy cattle: Where will it end?. J. Dairy Sci. 84: 1277-1293.

Marti, C. F., and D. A. Funk. 1994. Relationship between production and days open at different levels of herd production. J. Dairy Sci. 72:1682-1690.

Mercandante, M. E. Z., I. U. Packer, A. G. Razook, J. N. S. G. Cyrillo, and L.A. Figueiredo. 2003. Direct and correlated responses to selecting for yearling weight on reproductive performance of Nellore cows. J. Anim. Sci. 81:376-384.

Meyer, K., K. Hammond, P. F. Parnell, M. J. Mackinnon and S. Sivarajasingam. 1990. Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. Livest. Prod. Sci. 25:15-30.

Meyer, K. and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. Livest. Prod. Sci. 47:185-200.

Meyer, K. and M. Kirkpatrick. 2005. Up hill down dale: Quantitative genetics of curvaceus traits. Philos. Trans. R. Soc. B 360:1443-1455.

Nebel, R. L. and M. L. McGilliard. 1993. Interactions of high milk yield and reproductive performance in dairy cows. J. Dairy Sci. 76:3257-3268.

Nishida, A., M. A. Aziz, S. Nishida, and K. Suzuki. 2006. Modelling number of services per conception of Japanese Black cattle by random regression. J. Anim. Breed. Genet. 123:55-63.

Norman, H. D., J. R. Wright, S. M. Hubbard, R. H. Miller, and J. L. Hutchison. 2009. Reproductive status of Holstein and Jersey cows in the United States. J. Dairy Sci. 92:3517-3528.

Oseni, S., S. Tsuruta, I. Misztal, and R. Rekaya. 2004. Genetic parameters for days open and pregnancy rates in US Holsteins using different editing criteria. J. Dairy Sci. 87:4327-4333.

Philipsson, J. 1981. Genetic aspects of female fertility in dairy cattle. Livest. Prod. Sci. 8:307-319.

Powell, R. L. and H. D. Norman. 2006. Major advances in genetic evaluation techniques. J. Dairy Sci. 89:1337-1348.

Pryce, J. E., B. L. Nielsen, R. F. Veerkamp, and G. Simm. 1999. Genotype and feeding systems and interactions for health and fertility traits in dairy cattle. Livest. Prod. Sci. 57:193-201.

Raheja, K. L., E. B. Burnside, and L. R. Schaeffer. 1989. Relationship between fertility and production in Holstein dairy cattle in different lactations. J. Dairy Sci. 72:2670-2678.

Rust, T. and E. Groeneveld. 2002. Variance component estimation on female fertility traits in two indigenous and two European beef cattle breeds of South Africa. S. Afr. J. Anim. Sci. 32:23-29.

Schaeffer, L. R. 2004. Application of random regression models in animal breeding. Livest. Prod. Sci. 86:35-45.

Urioste, J. I., Y. M. Chang, H. Naya, and D. Gianola. 2007a. Genetic variability in calving success in Aberdeen Angus cows under extensive recording. Animal 1:8, pp 1081-1088.

Urioste, J. I., I. Misztal, and J. K. Bertrand.2007b. Fertility traits in spring-calving Aberdeen Angus cattle. 1. Model development and genetic parameters. J. Anim. Sci. 85:2854-2860.

Van der Werf, J. H. J., M. E. Goddard, and K. Meyer. 1998. The use of covariance functions and random regressions for genetic evaluation of milk production based on test day records. J. Dairy Sci. 81:3300-3308.

Van der Werf J. H. J. 2001. Random Regressions in Animal Breeding. Course notes available at: http://www-personal.une.edu.au/~jvanderw/ranregrcourse.htm. Accessed July 31, 2006.

Van der Westhuizen, R. R., S. J. Schoeman, G. F. Jordaan, and J. B. Van Wyk. 2001. Heritability estimates derived from threshold analysis for reproduction and stayability traits in a beef cattle herd. S. Afr. J. Anim. Sci. 31:25-32.

Van Doormaal, B. J., L. R. Schaeffer, and B. W. Kennedy. 1985. Estimation of genetic parameters for stayability in Canadian Holsteins. J. Dairy Sci. 68:1763-1769.

Van Raden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292.

Van Vleck, L. D. 1980. Stayability evaluation as a categorical trait and by considering other traits. J. Dairy Sci. 63:1172-11.

CHAPTER 2. GENETIC ANALYSIS OF DAYS OPEN USING A LINEAR LEGENDRE RANDOM REGRESSION MODEL

A paper to be submitted to Journal of Dairy Science

G.A. Gutierrez, M. H. Healey, and P.J. Berger

ABSTRACT

The objective of this study was to investigate the feasibility of using a linear Legendre random regression model for the analysis of female fertility as expressed by days open. The analysis provided insight about the kind and amount of variation over the trajectory for age at calving from 24 to 90 mo. An aging and genetic component of female fertility was discovered. Heritability ranged from 0.07 to 0.10 from 24 to 72 months. Permanent environmental correlations between fixed ages at calving changed from positive to negative values with greater distance between days open in young cows and days open in older cows; $r(24,36) = 0.88$, $r(24,72) = -0.65$. The random regression animal model is a better alternative to a repeatability animal model for estimation of variance components of days open. However, the assumption of genetic correlation of unity between adjacent parities is unrealistic. Further research is needed to evaluate the advantages of using random regression model on the genetic analysis of days open.

Key words: days open, random regression, female fertility.

INTRODUCTION

Genetic progress for milk yield has increased since 1960 due to the higher selection intensity for sires and higher reliability of sire's Predicted Transmitting Ability (PTA) from

modern progeny testing schemes (Powell and Norman, 2006). Female fertility, however, has declined in Holsteins (Lucy, 2001). Poor female fertility performance restricts the rate of genetic gain for milk yield, increases insemination costs, leads to premature culling, and reduces the overall milk yield per cow (Norman et al., 2009).

Female fertility of lactating cows is a very complex trait, it can be defined as the cow's ability to a) resume ovary function after calving, b) show a detectable estrus, c) become pregnant, and d) maintain pregnancy and succeed at calving. Therefore, many traits have been used as indicators of female fertility performance, e.g., days open (DO) (Dematawewa and Berger, 1998; Oseni et al., 2004; Gonzalez-Recio et al., 2006; Huang et al., 2007), number of services (Chang et al., 2006), or non-return rate (Heringstad et al., 2006). In 2003 a genetic evaluation of Holstein sires for daughter pregnancy rate (DPR) was implemented in United States (Van Raden et al., 2004). DPR is the predicted merit of sires after using DO as an independent variable followed by a transformation of scale.

Days open is defined as the interval from calving to conception. DO data in dairy cattle is characterized by having repeated measurements per cow and for being highly unbalanced due to involuntary culling for reasons such as reproductive failure, severe mastitis, death, etc. The unbalanced feature of DO data arise from the fact that an equal number of records were not available for all cows and that records were not taken at fixed time points. Nowadays, random regression models (RR) have been applied in the analysis of repeated measurement data where the trajectory of time was either days in milk, age or parity (e.g., daily milk yield, Bohmanova et al., 2008; beef growth rate, Arango et al., 2004; lamb growth, Fischer et al., 2004; number of services, Nishida et al., 2006).

Because a cow could have repeated days open (DO) records in her lifetime, DO can be analyzed as a function valued-trait (Meyer and Kirkpatrick, 2005) by using a Legendre polynomial random regression model (Schaeffer, 2004). RR modeling enables researchers to estimate mathematical functions (formally called covariance function (CF)) of the (co)variance between all possible points on the trajectory of time when each measurement is taken (Van der Werf, 2001). The CF is estimated from the (co)variance matrix of the RR coefficients (Meyer and Hill, 1997). The objective of this study was to estimate genetic parameters i.e., heritability (h^2), additive genetic variance, permanent environmental variance (PE), for DO by using a covariance function (CF)-random regression model.

MATERIALS AND METHODS

Data

Data in this study were from cows enrolled in a long-term sire selection project designed to explain the genetic change of milk in daughters of sires selected for either high or average PTA-fat plus protein yield. There were two concurrent lines: daughters of sires with high (HFP) or average (AFP) genetic merit for PTA fat plus protein yield. Cows from both lines were raised together at the Ankeny dairy research farm at Iowa State University (ISU) from 1986 to 2004. All cows were fed and managed as one herd, thus environmental differences between lines were limited. All replacement heifers were born at the farm. Herd composition was managed to be about 60% descendants of HFP and 40% descendants of AFP sires.

Three new sires were selected for each selection line every year from the official list of US active AI bulls. Sires were used two consecutive years to maintain an overlap between new and old sires in every contemporary group and were mated randomly within line. As a

result, progeny of 96 sires belonging to 16 generation groups were used in this research. Each

sire had on average 8 daughters.

Days open was calculated as the interval from last calving to conception date. Conception

date was confirmed by pregnancy check at 35 days after the last insemination date. The

voluntary waiting period was managed to be the same for both lines. Random mating was

practiced within line without regard for inbreeding. However, use of sires in either line was

dependent on semen availability and reasonable cost limits. Voluntary culling for low

production was allowed within line.

A total of 1852 DO records from Holstein cows (n=766) were used in the analysis. Data

were restricted to less than 6 parities. All cows were required to have a first parity record, but

not all cows had an opportunity to complete all parities due to death, culling or the ending of

data collection.

Pedigree of cows which had records was traced back for at least three generations, a total

of 1644 individuals in the pedigree file. The pedigree file was renumbered by using

RENUMF90 v1.7 (Misztal, 2005).

Statistical analysis

Data were analyzed using the following models: 1) a repeatability animal model (REP),

2) a random regression model (RR), and 3) a multiple trait model (MT). Preliminary analysis

were performed to determine the fixed effects affecting DO, residual variance homogeneity,

and the best order of fit for fixed regression to model the effect of age at calving on DO.

PROC GLM and PROC MIXED procedures implemented in SAS v 9.0 were used. Effects

of line of sire selection, year-season at calving, and parity were significant. There was

insufficient evidence to reject the hypothesis of homogeneous variance for DO across age at calving (mo). The linear regression on age at calving was the highest order polynomial that was significant. Thus, a linear Legendre polynomial was used in the fixed part of the REP and RR model.

The matrix notation of the REP model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wp} + \mathbf{e} \quad [1]$$

where $\mathbf{y}$ = a vector of days open records; $\mathbf{b}$ = a vector of fixed effects: line of sire selection (AFP or HFP), year-season (62 levels), parity (5 levels), and linear Legendre polynomial for age at calving; $\mathbf{a}$ = a vector of additive genetic effects (1644 levels); $\mathbf{p}$ = a vector of random permanent environmental effects; $\mathbf{e}$ = a vector of random residual effects; and $\mathbf{X, Z}$ and $\mathbf{W}$ = incidence matrices relating observations to fixed, additive genetic, and permanent environmental effects, respectively. The expectations were $E[y] = X_1 b$ and $E\begin{bmatrix} a \\ p \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$.

The Var (a) = $A\sigma_a^2$, Var (p) = $I\sigma_p^2$, and the Var (e) = $I\sigma_e^2$, where A = numerator relationship matrix and I = identity matrix. All covariance between random terms was assumed to be zero.

The variance components of the REP model were estimated by average information REML algorithm (AI-REML) implemented in ASREML v1.1 (Gilmour et al., 2002). The basic assumptions of the REP model were that repeated records of DO had a genetic correlation equal to 1 and a similar permanent environmental correlation.

The matrix notation of RR model was:

$$\mathbf{y} = \mathbf{X_2 b} + \mathbf{Z_2 \alpha} + \mathbf{W_2 \text{þ}} + \mathbf{e} \quad [2]$$

where $\mathbf{y}$ = a vector of days open records; $\mathbf{b}$ = a vector of fixed effects as defined above for model 1, $\boldsymbol{\alpha}$ = a vector of random linear Legendre polynomial coefficients for additive genetic

merit for each animal in the pedigree file, p = a vector of random linear Legendre polynomial coefficients for permanent environmental effects for each cow with records; e = a vector of random residual effects; $\mathbf{X_2}$ = an incidence matrix relating observations to fixed effects, $\mathbf{Z_2}$ and $\mathbf{W_2}$ = matrices of linear Legendre polynomial covariates (intercept and slope). The expectations were $E[y] = X_2 b$ and $E\begin{bmatrix} \alpha \\ p \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$, and the covariance structure of the RR

model was: $V\begin{bmatrix} \alpha \\ p \\ e \end{bmatrix} = \begin{bmatrix} A \otimes K_g & 0 & 0 \\ 0 & I \otimes K_p & 0 \\ 0 & 0 & R \end{bmatrix}$ [3], where A = numerator relationship matrix,

$\otimes$ is the symbol for kronecker product, K_g is the covariance matrix of the additive genetic random regression coefficients of order 2, K_p is the covariance matrix of the permanent environmental random regression coefficients of order 2, and $R = I\sigma_e^2$.

The covariance function (CF) for the additive genetic or the permanent environmental effects was: $CF = \Phi K \Phi^T$ [4], where Φ = linear Legendre polynomial coefficient matrix for standardized units of age at calving in months (Schaeffer, 2004) and K is either the covariance matrix of the random regression coefficients for the additive (K_g) or permanent environmental effect (K_p). K_g and K_p were estimated by AI-REML algorithm implemented in ASREML v1.1 (Gilmour et al., 2002). In order to solve convergence problems the correlation between additive random intercept and slope was fixed at 0.99 by ASREML. The eigenfunctions (EF) of K_g and K_p were obtained by $EF = \Phi E$ [5], where E was the eigenvector of either K_g or K_p. The CF was used to estimate both the monthly additive genetic and permanent environmental (co)variances across the trajectory of age at calving from 20 to 90 months.

Each observation for DO at a different parity was considered as a different trait in MT model. The matrix notation of MT model was:

$$\mathbf{y} = \mathbf{X_3 b} + \mathbf{Z_3 a} + \mathbf{e} \qquad [6]$$

where $\mathbf{y}$ = a vector of records for days open assumed to be continuously distributed; $\mathbf{b}$ = a vector of fixed effects including: line of sire selection (AFP or HFP), age at calving (mo) of cows as a covariate, year-season at calving for each parity (61, 56, 46, 34 and 23 levels of year-four month intervals from 1988 to 2004 for parity 1 to 5, respectively); $\mathbf{a}$ = a vector of random additive genetic animal effects (1644 levels for each parity); $\mathbf{e}$ = a vector of random residual effects; and $\mathbf{X_3}$ and $\mathbf{Z_3}$ = incidence matrices relating observations to fixed, and random additive genetic, respectively. The $E\begin{bmatrix} y \\ a \\ e \end{bmatrix} = \begin{bmatrix} X_3 b \\ 0 \\ 0 \end{bmatrix}$ and $V\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$ [7] where E and V are the expectation and variance operators, respectively. Matrix $G = A \otimes G_0$, where A is the numerator relationship matrix of additive genetic effects, and G_0 is a matrix (5x5) of additive genetic (co)variances. Matrix $R = I \otimes R_0$, where I is an identity matrix and R_0 is a matrix (5x5) of (co)variances between residual effects for the 5 traits.

The variance components were estimated by Gibbs sampling implemented in THRGIBBS1F90 (Tsuruta and Misztal, 2006). POSTGIBBSSF90 and a visual inspection of trace plots for a chain of 200,000 samples were used to determine the burn-in length, number of samples and thinning ratio. A degree of belief of 7 (number of traits plus two) was assigned to the starting values of variance components. A chain of 200,000 samples was used to obtain a set of 180 samples after burn-in of 20,000 samples, keeping every 1,000th sample. The saved samples were used to obtain the posterior mean and posterior standard deviation of variance components, heritability, and genetic correlation.

Narrow sense heritability (h^2) and repeatability (r) were estimated in both RRM and REP

models by $h^2 = \dfrac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_p^2 + \sigma_e^2\right)}$ [8] and $r = \dfrac{\left(\sigma_a^2 + \sigma_p^2\right)}{\left(\sigma_a^2 + \sigma_p^2 + \sigma_e^2\right)}$ [9]. For the estimation of h^2 in

MT model, σ_p^2 was omitted from [8].

In the RR model, the breeding value of DO for animal k at month j was estimated by

$EBV_{kj} = t\,\hat{a}_k$ [10]; where t was a vector containing the Legendre polynomial elements at

month j and $\hat{a}_k$ was the vector of the additive random coefficients solutions for animal k.

Cows were intentionally mated to sires at random with attention to see that the same

service sire was used for repeated services to the same cow. However, not all heifers and

cows were inseminated with the same sire in all services at a given parity, so their fertility

could have been affect by more than one sire. Thus, an effect for service sire was not

included in all models due to the difficulty of accounting for the different sires that had been

used in insemination events until a cow got pregnant or was culled, and there was a no clear

way of incorporating time-dependent service sire effect in the statistical models as others

have found (Pryce et al., 1999; Chang et al., 2006).

RESULTS AND DISCUSSION

Descriptive analysis

Means and standard deviations for DO and age at calving are given in Table 1. By

definition, heifers (parity = 0) do not have a value for DO. Thus only proven fertile heifers

become lactating cows where DO becomes available. This may be a criticism of DO as a

measure of fertility early in the reproductive life of dairy cows, because it does not address the dual nature of fertility, i.e., conception and the ability to maintain pregnancy in heifers.

There was an increasing phenotypic trend for DO in both selection lines with age at calving. In fact the fixed regression line had a positive intercept and slope. The average DO for HFP cows was slightly higher than the average for AFP cows (151 versus 148 days, respectively), but previous statistical analysis showed no significant (p≥0.05) difference between selection lines for DO. The percentage of cows remaining in the herd after each calving tended to decrease with parity due to greater involuntary culling among older aged cows. This DO data set was highly unbalanced and skewed to the right because cows tended to have more DO records at earlier ages. Others found a similar pattern for the distribution of DO data in dairy cattle (Van Raden et al., 2004; González-Recio et al., 2006).

Table 1. Number of cows, days open mean (s.d.), age at calving mean (s.d.), and percentage of remaining cows by line and parity.

Line	Parity	N	Days open $\bar{X}$ (s.d.)	Age at calving (mo) $\bar{X}$ (s.d.)	Remaining cows (%)
AFP	1	335	140.3 (85.6)	25.1 (2.2)	74.8*
	2	228	146.2 (82.0)	38.5 (3.3)	68.1
	3	134	159.7 (81.9)	52.2 (4.6)	58.8
	4	69	157.4 (80.4)	65.3 (5.9)	51.5
	5	27	174.3 (97.4)	77.4 (3.7)	39.1
HFP	1	431	147.2 (90.2)	25.1 (2.2)	71.7*
	2	300	152.5 (84.5)	38.7 (3.4)	69.6
	3	188	157.3 (87.9)	52.4 (4.4)	62.6
	4	100	149.2 (87.3)	65.2 (4.8)	53.2
	5	40	157.0 (84.5)	78.1 (5.1)	40.0

*Number of cows that calved at first parity was 448 and 601 for AFP and HFP, respectively.

Log likelihoods

The -2log likelihood for RR (17685.5) was lower than the REP model (17700.7) and the likelihood ratio test was significant (p<0.05). Thus, despite of having a convergence problem and a higher number of parameters, RR model performed better than REP model to estimate variance components and to predict random effects for DO.

The RR model had an order of fit of 2 for both additive genetic and permanent environmental effects. Some researchers have found that an order of fit of 2 was appropriate to model the Legendre polynomial regression for additive genetic effects of growth traits in beef cattle (Meyer and Hill, 1997; Arango et al., 2004) and dairy cattle (Koenen and Veerkamp, 1998), ultra-sound muscle area (Hassen et al., 2003 and 2004), daily milk yield (Van der Werf et al., 1998, Pool et al., 2000). Others, however, have found an order of fit higher than 2 was appropriate to model random regression for additive genetic effects of growth traits in beef cattle (Meyer, 1999) and dairy cattle (Veerkamp and Thompson, 1999), milk yield in dairy cattle (Olori et al., 1999; Hammami et al., 2008), and number of services in beef cattle (Nishida et al., 2006).

It seems that a high-order polynomial was required to model random regression for permanent environmental effects in different traits and species (Arango et al., 2004; Meyer, 1999; Hassen et al., 2003; Meyer and Kirkpatrick, 2005), though no attempt was made to use order of fit higher than 2 due to convergence problems.

Eigenvalues and eigenfunctions

Eigenvalues and eigenfunctions obtained in RRM are given in Table 2 and Figure 1, respectively. The magnitude of the eigenvalue relative to the trace of the CF coefficient matrix indicates the amount of variation that is explained by factors associated with each eigenvalue. A large eigenvalue indicates that the change caused by selection of the associated eigenfunction will happen faster. The trend of eigenfunctions is an indication of how the factors associated with each eigenvalue affects the pattern of variation at all ages (Meyer and Kirkpatrick, 2005).

Table 2. Eigenvalues and their proportions for the additive genetic and permanent environment covariance function.

	Eigenvalues			Proportion of total (%)	
	First	Second	Total	First	Second
Additive genetic	667.84	0.06	667.90	99.99	0.01
Permanent environment	2064.11	152.44	2216.55	93.12	6.88

The first eigenvalue accounted for about 99.99% of the additive genetic variation of DO at all ages and its corresponding eigenfunction tended to slightly decrease from about -0.5 to -0.9 with age at calving. The latter may be a consequence of using a genetic correlation about unity to solve convergence problems in RRM. The leading eigenvalue was approximately constant over the cow's lifetime suggesting that the additive genetic variation was explained by a genetic factor acting similarly on all ages. Therefore, selection for the first eigenfunction may decrease DO at all ages.

The second eigenvalue accounted for 0.01% of total additive genetic variance. Its' corresponding eigenfunction tends to decrease across ages from about 1.6 to -1.0. The change of sign suggests that an associated factor to the second eigenvalue may have opposite effects

on DO at younger and older ages. Although, response to selection based on the second eigenvalue will be very small, it can be used to select for lower DO at later ages.

The first and second eigenfunctions explained 93% and 7% of the permanent environmental variance, respectively. Both eigenfunctions had steep trends but at different rates of change. The leading eigenfunction changed in sign across age which is in agreement with the change in the magnitude and sign of PE correlation depending on the lag (distance) between pairs of selected ages. More will be discussed in section about PE correlations.
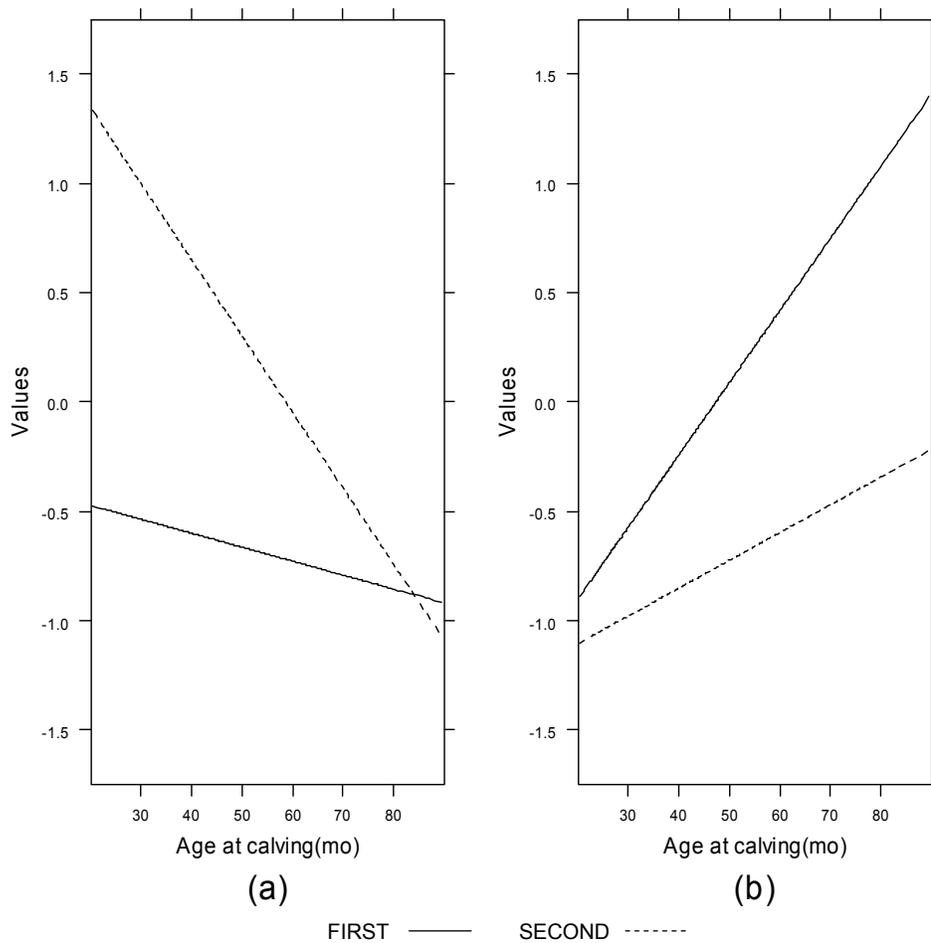
Figure 1. Eigenfunctions of (a) additive genetic and (b) permanent environment covariance function coefficient matrix.

Variance component estimates

Estimates of variance components for the REP model were 512.9, 84.6, and 6067.6 d^2 for additive genetic, permanent environmental and residual effects, respectively. Heritability and repeatability estimates were 0.08 and 0.09, respectively.

The estimates of variance components obtained from the RR model were the co(variance) matrix of the random regression coefficients for the additive genetic (K_g) and permanent environmental effects (K_p):

$$K_g = \begin{bmatrix} 1292.3 & 136.7 \\ 136.7 & 14.5 \end{bmatrix}, \; K_p = \begin{bmatrix} 798.0 & 739.7 \\ 739.7 & 1211.2 \end{bmatrix}, \; \text{and a residual variance of 5589.6 } d^2.$$

The RR model allows one to study the change in (co)variance with age. K_g and K_p were used to calculate the CF for additive and permanent environmental effects. These CFs were used separately to calculate the (co)variance curves and correlation between any two DO records measured at given ages for the additive and permanent environmental effects.

Figure 2 gives the change in additive and permanent environmental variance over the trajectory of age at calving from 20 to 90 mo. The additive genetic variance tended to increase slightly with age at calving. The permanent environmental variance, however, tended to be higher at extremely younger and older ages at calving. The lowest value of PE variance was found at an intermediate age at calving of 44 mo. These values need to be interpreted with caution, because permanent environmental variance may have been overestimated near the edges of the trajectory due to limited amount of data at extreme ages and lack of asymptotic properties of the Legendre polynomial (Arango et al., 2004; Bohmanova et al., 2008).

Table 3 gives heritability, fraction of permanent environmental variance and repeatability at fixed ages at calving. In RR model, the additive genetic variance tended to increase with age at calving (Figure 2), but heritability estimates increased only slightly from 24 to 72 months as shown in Table 3. The fraction of phenotypic variance explained by permanent environmental variance varied from 0.03 to 0.19 across the 5 fixed ages and repeatability estimates ranged from 0.17 to 0.29. Figure 3 shows the change of heritability (h^2) and the fraction of phenotypic variance due to permanent environmental effect (FPE) with ages at calving.
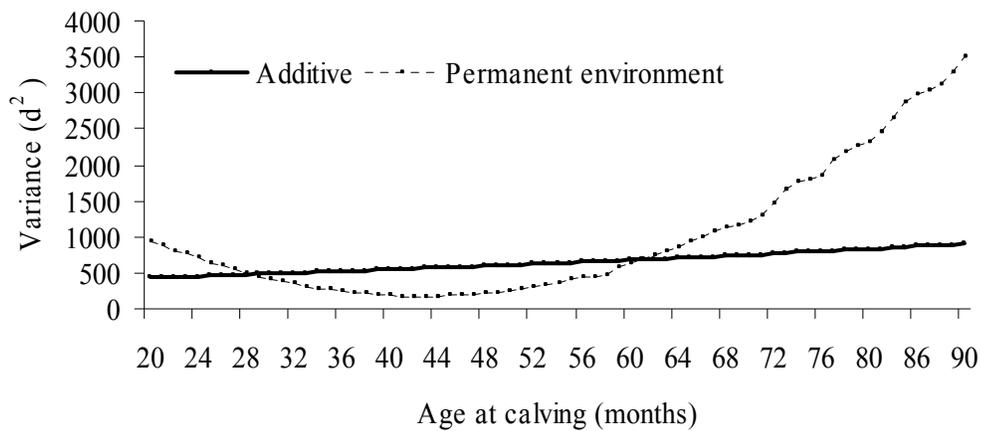
Figure 2. Additive and permanent environmental variances for days open.

Table 3. Additive variance (σ_a^2), permanent environmental variance (σ_{pe}^2), heritability (h^2), fraction of phenotypic variance explained by permanent environmental effect (FPE), and repeatability for days open by random regression model.

Age at calving (mo)	σ_a^2	σ_{pe}^2	h^2	FPE	Repeatability
24	451.41	709.07	0.07	0.11	0.17
36	523.00	241.82	0.08	0.04	0.12
48	599.49	215.35	0.09	0.03	0.13
60	681.42	672.89	0.10	0.09	0.19
72	767.76	1470.01	0.10	0.19	0.29
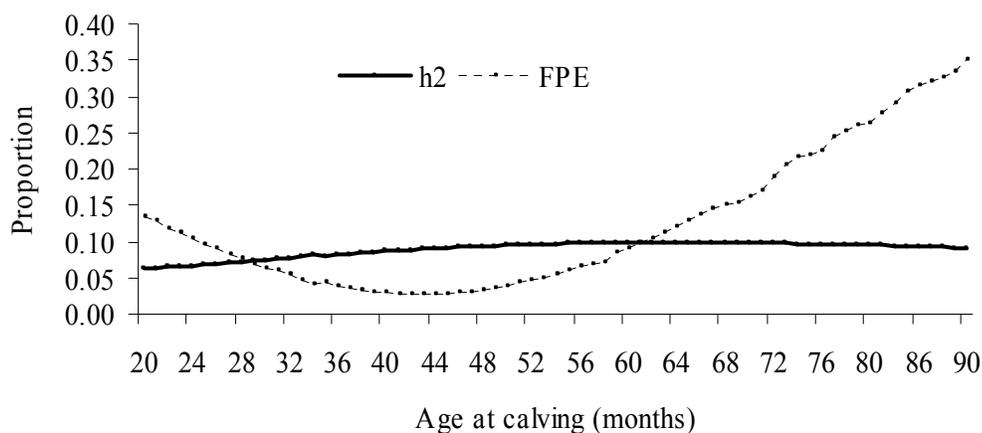
Figure 3. Heritability (h^2) and the fraction of phenotypic variance attributed to permanent environmental effects (FPE) for days open.

Theoretically, repeatability is defined as the proportion of phenotypic variance due to additive genetic, non-additive genetic, and permanent environmental effects (Hohenboken, 1985). The operational statistical model used in the repeatability model, however, did not allow partitioning of non-additive genetic from the permanent environmental component (Mrode, 2005). Therefore, what we called PE is the sum of both non-additive genetic and permanent environmental effects. In addition, PE is not constant across the trajectory of age

at calving; implying that non-additive genetic effects or permanent environmental effects may not similarly affect DO at all ages.

Table 4 gives the variance components and heritability estimates for DO obtained by a MT model. The posterior mean estimate of the additive genetic variance tends to increase with parity. On the other hand the posterior mean estimate of the residual variance tends to decrease from parity 1 to 3, after parity 3 it tends to increase up to parity 5. The posterior mean of heritability for DO tends to increase with parity. Heritability estimates for DO in different parities are scarce in the literature, maybe due to the difficulty in implementing a multiple trait analysis for DO (Jansen et al., 1987). Others found that heritability estimates for DO tended to slightly increase with parity (Berger et al., 1981; Jansen et al., 1987; Raheja et al., 1989).

The estimates of the additive genetic variance, residual variance and heritability for DO from MT model are higher than their corresponding estimates from RRM. However, a similar increasing trend with parity for additive genetic variance and heritability was found in RR and MT model.

Table 4. Posterior means (s.d.) of additive variance (σ_a^2), residual variance (σ_e^2), and heritability (h^2) for days open by multiple trait model.

Parity	Age at calving (mo)	σ_a^2	σ_e^2	h^2
1	25	1178.7(322.7)	6117.6(419.4)	0.16(0.04)
2	39	1413.2(441.5)	5315.5(509.9)	0.21(0.06)
3	52	2920.4(697.5)	4421.4(658.8)	0.40(0.08)
4	65	4749.8(1399.9)	4488.2(940.9)	0.51(0.10)
5	77	6608.6(2522.8)	9000.1(3441.1)	0.43(0.12)

Genetic and permanent environmental correlations

Genetic correlation between any pair of ages was 0.99, this was a result of setting the correlation between the additive genetic intercept and slope equal to 0.99. The permanent environmental correlations were highly variable as shown in Figure 4. For example, the PE correlations between 24 and 36, 48, 60, and 72 months were 0.88, 0.06, -0.48, and -0.65, respectively. Thus, correlations between permanent environmental effects changed from positive to negative values with greater distance between days open in young cows and days open in older cows. In addition PE correlation between different ages at calving were not stationary, for example two correlations with lag 12 mo were different, r (24, 36 mo) = 0.88 and r(60,72 mo) = 0.98.

These differences in PE correlations would suggest that environmental effects or non-additive genetic effects were not constant with age at calving. Some environmental factors that affect repeated records on the same animal seem to be semi-permanent rather than permanent effect (Hohenboken, 1985). For instance, a factor may affect DO at adjacent parities to a different extent.

A few studies have reported estimates of non-additive genetic effects on female fertility in dairy cattle. The sum of dominance and additive by additive variance had equal or greater values than additive genetic variance for DO (Hoeschele, 1991), calving interval (Fuerst and Solkner, 1994) and the interval from calving to first insemination (Palucci et al., 2007).

It was found that non-additive genetic effects contributed more than additive genetic and permanent environmental effects to the phenotypic variance for the interval from calving to first insemination (ICFI). Also, permanent environmental effects showed a negligible contribution to the phenotypic variance for ICFI (Palucci et al., 2007). Therefore, changes in

expression of non-additive genetic effects with age may explain the changes in estimates of

PE correlations over the trajectory of age at calving from 24 to 72 mo.

Table 5 gives the posterior mean of genetic and phenotypic correlations for DO in

different parities from a MT model. Genetic correlations for DO between different parities

were positive and varied from low to moderate in most cases, but genetic correlations

between parities 2 and 4, and 2 and 5 were high.   In one study, genetic correlations between

DO in different lactations were positive and ranged from moderate to high (Jansen et al.,

1987). Conversely, in another study genetic correlations for DO in different parities were

positive and close to zero (Raheja et al., 1989).
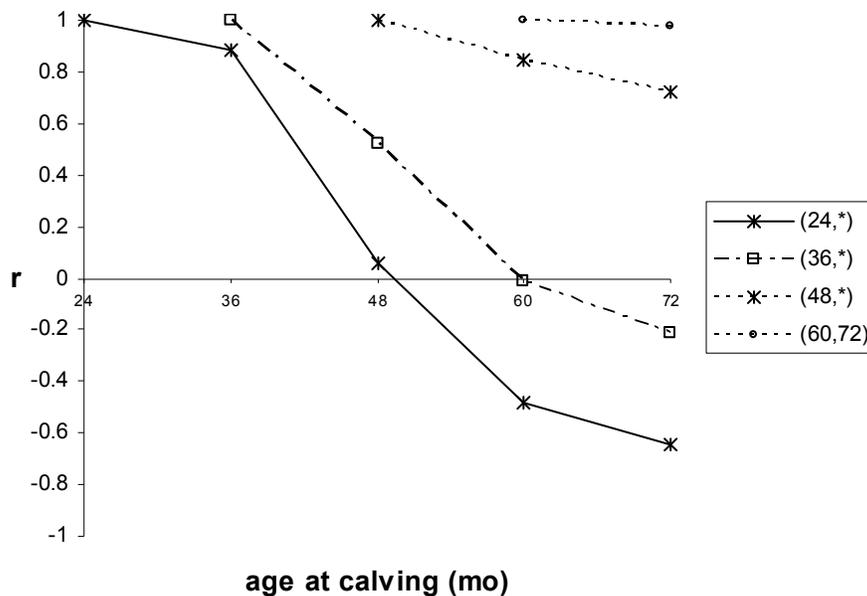
Figure 4.   Permanent environmental correlations between pairs of selected ages at 24, 36, 48, 60 and 72 age at calving (mo).

Table 5. Posterior means(s.d.) of genetic (above diagonal) and phenotypic (below diagonal) correlations for days open in different parities by multiple trait model.

Parity	1	2	3	4	5
1	.	0.20(0.20)	0.15(0.21)	0.26(0.20)	0.28(0.25)
2	0.15(0.07)	.	0.29(0.18)	0.59(0.16)	0.57(0.20)
3	-0.09(0.09)	0.06(0.09)	.	0.33(0.19)	0.28(0.24)
4	0.04(0.10)	0.22(0.12)	0.23(0.11)	.	0.36(0.20)
5	0.16(0.17)	0.23(0.17)	0.15(0.17)	0.36(0.12)	.

Additive random coefficient solutions and breeding values estimates

The random coefficient solutions of all animals in the pedigree file were obtained from the animal RR model with similar order of fit 2 for the fixed-averaged curve, additive genetic, and permanent environmental effects, but only solutions for cows with records and their sires are described in this section. Random intercept and slopes for the additive genetic effect of both sires and cows were highly correlated (r=0.99), therefore the sign and magnitude of the additive random intercept determined the rank order of individuals based on their estimated breeding value (EBV) for DO. The genetically superior animals for DO were identified by having a negative intercept and slope.

Estimated monthly breeding values for days open were determined by using equation [10], so each individual had a linear profile of their monthly breeding value with age at calving. Only breeding values from 24 to 84 month are presented here. Ranking of sires and cows based on their monthly EBV did not change with age, moreover, differences in EBV tended to be larger at later ages than at earlier ages. Monthly EBV of sires were more variable in the HFP than AFP line (data not shown), although the difference between lines was not significant (p<0.05).

The monthly EBV profiles for 12 selected sires are shown in Figure 5. These sires were chosen regardless of selection lines to identify upper, intermediate, and lower rank sires according to their additive genetic intercept values. The best sires have a steep declining breeding value profile.
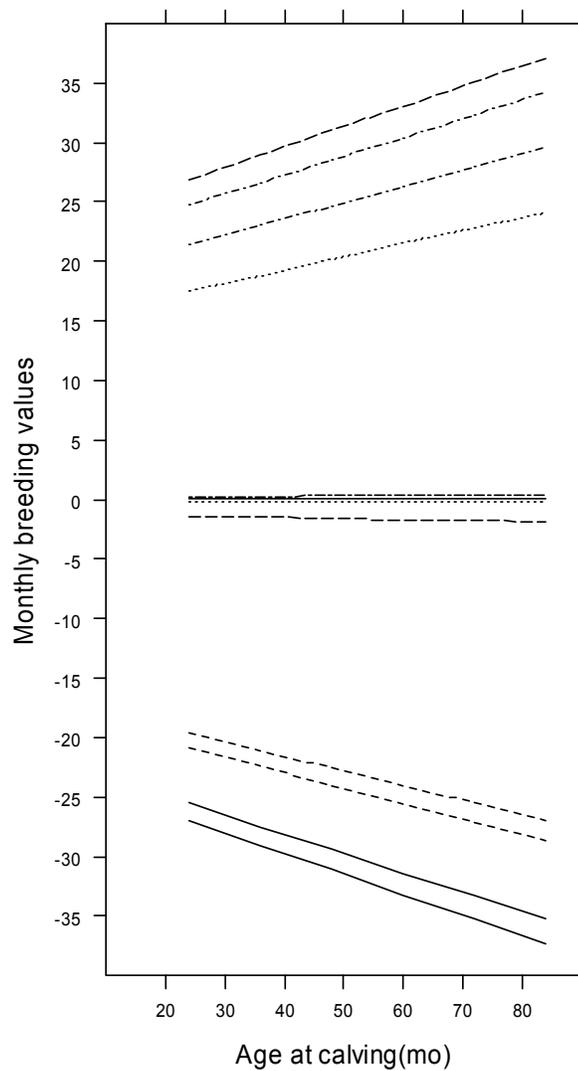
Figure 5. Profiles of estimated DO monthly breeding values for 12 sires (4 top, 4 intermediate and 4 bottom).

Daughters of the 4 best sires showed on average better performance for fertility, as expressed in DO, than daughters of the 4 worst sires. Table 6 gives the distribution of daughter records for DO for sires across the 3 groups. The 55% of daughters of the 4 best sires had 3 or more DO records during their lifetime, whereas only 39% of the daughters of the 4 worst sires had 3 or more DO records during their lifetime. Also, 23% of daughters of the 4 best sires showed DO records less than 100 d during their lifetime, whereas 12% of the daughters of the 4 worst sires showed DO records less than 100 d during their lifetime.

Besides EBV profiles of daughters of the 4 best sires were far below the fixed average curve, thus it is an indication that the RR model provides valid breeding values for sires. We believe this is a confirming evidence validating RR as a useful model for predicting conception and maintenance of pregnancy.

General discussion

The data used in this analysis came from a unique designed dairy breeding experiment at ISU in US, only comparable with a selection experiment completed at Langhill Dairy Cattle Research Center in Scotland from 1988 to 1996 (Pryce et al., 1999). In both experiments, researchers sought to evaluate the effect of selection for PTA-fat plus protein yield on milk composition traits, but also the Langhill experiment was designed to evaluate feeding systems and a genotype by feeding system interaction. Selection for high genetic merit at Langhill resulted in deterioration in days open (Pryce et al., 1999), which is not in agreement with this study.

Table 6. Daughters' fertility performance of 12 selected sires

Sire Group	Sire ID	# daughters/sire	% daughters with		
			more than 3 DO records	all DO records less than 100 days	all DO records less than 250 days
Best	1797719	12	67	25	83
Best	1811342	15	40	47	67
Best	2009164	9	44	0	89
Best	2116771	8	75	0	75
Best	All four	44	55	23	77
Intermediate	1983348	12	42	8	75
Intermediate	2264535	5	0	20	100
Intermediate	1895040	10	60	40	80
Intermediate	2109915	6	0	33	83
Intermediate	All four	33	33	24	82
Worst	1958361	16	69	13	50
Worst	2203438	9	0	0	33
Worst	2152960	7	0	0	29
Worst	1896613	9	56	33	78
Worst	All four	41	39	12	49

The reasons for this discrepancy could be attributed to differences in populations, experiment design and environmental factors such as management practices. The two populations differed on their origin (UK vs USA), number of generation of cows (Data from 8 years after selection starts were used at Langhill whereas all data at ISU were included in our analysis), heifers selection procedures (selection base on pedigree index for FP at Langhill whereas heifers were not selected for FP at ISU), and number of sires used per generation (4 to 5 vs. 3 sires per line at Langhill and ISU, respectively).

In addition, variance component estimates for DO have been reported to be highly influenced by management practices and editing procedures (Oseni et al., 2004). The farm manager may delay insemination date in early lactation when the cow had high milk yield or

heat stress in summer, thus longer DO were recorded due to management practices and it would bias variance component estimates. Besides, the change of upper limit of DO affected the estimation of the additive genetic variance, for instance lowering the upper limit from 305 to 250 increases the additive genetic variance of DO at first parity (Oseni et al., 2004).

 Another possible reason for not finding differences on DO between lines may be sampling error. It is possible that chosen sires at ISU project did not differ in breeding values for female fertility (Daughter pregnancy rate) because they were not selected for this trait.

The heritability estimates from REP, RR and MT models were higher than those reported previously in the literature accounting for repeated records of DO. Heritability estimates of DO from field data using similar edititing criteria and repeatability animal model were 0.04 (Dematawewa and Berger, 1998; Van Raden et al., 2004; Gonzales-Recio and Alenda, 2005). In contrast, the heritability estimate for DO from another experimental farm, such as Langhill, was 0.13 using a repeatability animal model. It was not surprising to get higher heritability estimates from designed experiment data than from field data because environmental factors (e.g. management, feeding, health care) were better controlled in designed experiments. To our knowledge nobody has reported heritability estimates of DO using RR model.

Repeatability estimates from both REP and RR models were closer than those reported in the literature. Previous repeatability values varied from 0.05 to 0.13 (Dematawewa and Berger, 1998; Van Raden et al., 2004), which agrees with our results using REP model and intermediate ages (36 to 48 months) using RR model. In contrast, FPE was lower than those inferred from the literature using a repeatability model. FPE obtained in this study was 0.01

whereas 0.08 to 0.09 were inferred from previous work (Dematawewa and Berger, 1998; Van Raden et al., 2004).

Both REP and RR models used in our study to estimate variance components for DO had the assumption of genetic correlation close to unity between repeated observations on the same cow. However, genetic correlations estimates from MT model ranged from low to moderate. The difference between estimates of variances components obtained from RR and MT models are due to differences in assumptions. For instance, the example of a cow calving at 32 mo for the first versus the second parity, would be treated as the same genetic trait in the RR model, but as a different trait in the MT model (Dekkers, 2009, personal communication).

The RR model had advantages over the REP model on its ability to predict changes in the additive genetic effects and permanent environmental effects with age at calving. Also, the RR model takes into account missing observations for each animal in breeding value estimation, but it does not discriminate for the reasons explaining why cows left the herd, thus involuntary culling was assumed to be the reason for dropouts, but some cows will leave the herd due to reproductive failure (e.g. chronic cystic follicular degeneration). However, further research is needed to validate the RRM using field data. Future investigation may focus on editing procedures, additional fixed effects and modeling permanent environmental effects.

CONCLUSIONS

The linear Legendre random regression animal model is a better alternative to a repeatability animal model for estimation of variance components for days open. However,

the assumption of genetic correlation of unity is not realistic for both models. Further

research is needed to evaluate the advantages of using random regression model on the

genetic analysis of days open using field data.

REFERENCES

Arango, J. A., L. V. Cundiff, and L. D. Van Vleck. 2004. Covariance functions and random regression models for cow weight in beef cattle. J. Anim. Sci. 82:54-67.

Berger, P. J., R. D. Shanks, A. E. Freeman and R. C. Laben. 1981. Genetics aspects of milk yield and reproductive performance. J. Dairy Sci. 64:114-122.

Bohmanova, J., F. Miglior, J. Jamrozik, I. Misztal, and P. G. Sullivan. 2008. Comparison of random regression models with Legendre polynomials and linear splines for production traits and somatic cell score of Canadian Holstein cows. J. Dairy Sci. 91:3627-3638.

Chang, Y. M., I. M. Andersen-Ranberg, B. Heringstad, D. Gianola, and G. Klemetsdal. 2006. Bivariate analysis of number of services to conception and days open in Norwegian Red using a censored threshold-linear model. J. Dairy Sci. 89:772-778.

Dematawewa, C. M. B., and P. J. Berger. 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins. J. Dairy Sci. 81:2700-2709.

Fischer, T. M., J. Van der Werf, R. G. Banks, and A. J. Ball. 2004. Description of lamb growth using random regression on field data. Livest. Prod. Sci. 89:175-185.

Fuerst C., and J. Solkner. 1994. Additive and nonadditive genetic variance for milk yield, fertility, and lifetime performance traits of dairy cattle. J. Dairy Sci. 77:1114-1125.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. ASREML User Guide Release 1.0. VSN International Ltd, Hemel Hempstead, HP11ES, UK.

González-Recio, O. and R. Alenda. 2005. Genetic parameters for female fertility traits and a fertility index in Spanish dairy cattle. J. Dairy Sci. 88:3282-3289.

González-Recio, O. Y., M. Chang, D. Gianola, and K. A. Weigel. 2006. Comparison of models using different censoring scenarios for days open in Spanish Holstein cows. Anim. Sci. 82:233-239.

Hammami, H., B. Rekik, H. Soyeurt, A. Ben Gara, and N. Gengler. 2008. Genetic parameters of Tunisian Holsteins using a test-day random regression model. J. Dairy Sci. 91:2118-2126.

Hassen, A., D. E. Wilson, and G. H. Rouse. 2003. Estimation of genetic parameters for ultrasound-predicted percentage of intramuscular fat in Angus cattle using random regression models. J. Anim. Sci. 81:35-45.

Hassen, A., D. E. Wilson, and G. H. Rouse. 2004. Partitioning variances of growth in ultrasound longissimus muscle area measures in Angus bulls and heifers. J. Anim. Sci. 82:1272-1279.

Heringstad, B., I. M. Andersen-Ranberg, Y. M. Chang, and D. Gianola. 2006. Short communication: Genetic analysis of non-return rate and mastitis in first-lactation Norwegian Red cows. J. Dairy Sci. 89:4420-4423.

Hohenboken, W. D. 1985. II. Genetics at the level of population. In: General and Quantitative Genetics. Ed. A. B. Chapman. World Animal Science Series, A4. Elsevier Science, New York.

Hoeschele, I. 1991. Additive and nonadditive genetic variance in female fertility of Holsteins. J. Dairy Sci. 74:1743-1752

Huang, C., I. Misztal, S. Tsuruta, and T. J. Lawlor. 2007. Methodology of evaluation for female fertility. Interbull Bulletin 37:156-159.

Jansen, J., J. Van der Werf, and W. de Boer. 1987. Genetic relationships between fertility traits for dairy cows in different parities. Livest. Prod. Sci. 17:337-349.

Koenen, E. P. and R. F. Veerkamp. 1998. Genetic covariance functions for live weight, condition score, and dry matter intake of lactating Holstein-Friesian heifers. Livest. Prod. Sci. 57:67-77.

Lucy, M. C. 2001. Reproductive loss in high-producing dairy cattle: Where will it end?. J. Dairy Sci. 84:1277-1293.

Meyer, K. and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. Livest. Prod. Sci. 47:185-200.

Meyer, K. 1999. Estimates of genetic and phenotypic covariance functions for postweaning growth and mature weight of beef cows. J. Anim. Breed. Genet. 116:181-205.

Meyer, K. and M. Kirkpatrick. 2005. Up hill down dale: Quantitative genetics of curvaceus traits. Philos. Trans. R. Soc. B 360:1443-1455.

Misztal, I. 2005. Renumf90-renumbering program for BLUPF90 family. Technical note available at: http://nce.ads.uga.edu/~ignacy/numpub/blupf90/docs/Readme.renumf90. Accessed March 03, 2009.

Mrode, R. A. 2005. Linear models for the prediction of animal breeding values. 2nd. ed. CABI International, Wallingford, UK.

Nishida, A., M. A. Aziz, S. Nishida, and K. Suzuki. 2006. Modelling number of services per conception of Japanese Black cattle by random regression. J. Anim. Breed. Genet. 123:55-63.

Norman, H. D., J. R. Wright, S. M. Hubbard, R. H. Miller, and J. L. Hutchison. 2009. Reproductive status of Holstein and Jersey cows in the United States. J. Dairy Sci. 92:3517-3528.

Olori, V. E., W. G. Hill, B. J. McGuirk, and S. Brotherstone. 1999. Estimating variance components for test day milk records by restricted maximum likelihood with a random regression animal model. Livest. Prod. Sci. 61:53-63.

Oseni, S., S. Tsuruta, I. Misztal, and R. Rekaya. 2004. Genetic parameters for days open and pregnancy rates in US Holsteins using different editing criteria. J. Dairy Sci. 87:4327-4333.

Palucci, V., L. R. Schaeffer, F. Miglior, and V. Osborne. 2007. Non-additive genetic effects for fertility traits in Canadian Holstein cattle. Genet. Sel. Evol. 39:181-193.

Pool, M. H., L. L. G. Janss, and T. H. E. Meuwissen. 2000. Genetic parameters of Legendre polynomials for first parity lactation curves. J. Dairy Sci. 83:2640-2649.

Powell, R. L. and H. D. Norman. 2006. Major advances in genetic evaluation techniques. J. Dairy Sci. 89:1337-1348.

Pryce, J. E., B. L. Nielsen, R. F. Veerkamp, and G. Simm. 1999. Genotype and feeding systems and interactions for health and fertility traits in dairy cattle. Livest. Prod. Sci. 57:193-201.

Raheja, K. L., E. B. Burnside, and L. R. Schaeffer. 1989. Relationship between fertility and production in Holstein dairy cattle in different lactations. J. Dairy Sci. 72:2670-2678.

Schaeffer, L. R. 2004. Application of random regression models in animal breeding. Livest. Prod. Sci. 86:35-45.

Tsuruta, S., and I. Misztal. 2006. THRGIBBS1F90 for estimation of variance components with threshold-linear models. Commun. 27-31 in Proc. 8th World Congress Gen. Appl. Livest. Prod. Belo Horizonte, Brazil.

Van der Werf, J. H. J., M. E. Goddard, and K. Meyer. 1998. The use of covariance functions and random regressions for genetic evaluation of milk production based on test day records. J. Dairy Sci. 81:3300-3308.

Van der Werf J. H. J. 2001. Random Regressions in Animal Breeding. Course notes available at: http://www-personal.une.edu.au/~jvanderw/ranregrcourse.htm . Accessed July 31, 2006.

Van Raden, P. M., A.H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292.

Veerkamp, R. F. and R. Thompson. 1999. A covariance function for feed intake, live weight, and milk yield estimated using a random regression model. J. Dairy Sci. 82:1565-1573.

CHAPTER 3. GENETIC ANALYSIS OF CALVING SUCCESS IN DAIRY CATTLE

A paper to be submitted to Journal of Dairy Science

G.A. Gutierrez, M. H. Healey, and P.J. Berger

ABSTRACT

The objective of this study was to investigate genetic parameters for calving success (CS) at different parity groups. CS was defined either as a binary trait (CS-B) or an ordered categorical variable (CS-T). CS-B had two categories (1=success and 2=failure). Two definitions of CS as a three categorical trait were used, CS-T (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) and CS-T2 (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve). Data from 1236 Holstein females from parity 0 to 5 were analyzed with threshold animal model. Posterior means of heritability for CS-B from parity 0 to 5 were slightly lower than those for CS-T. Posterior means of heritability for CS-B were 0.16(.08), 0.08(.03), 0.23(.07), 0.23(0.07), 0.24(.08) and 0.17(.08) for parity 0 to 5, respectively. Posterior means of heritability for CS-T were 0.17(.08), 0.10(.03), 0.21(.06), 0.22(0.07), 0.28(.08) and 0.21(.08) for parity 0 to 5, respectively. Posterior means of heritability for CS-T2 were 0.10(.07), 0.09(.04), 0.29(.06), 0.27(0.08), 0.24(.08) and 0.30(.09) for parity 0 to 5, respectively. Posterior means of genetic correlations between adjacent calving opportunities for CS-B, CS-T, and CS-T2 were variable in sign and magnitude with high posterior standard deviations. Phenotypic correlations between adjacent parities for CS-B, CS-T, and CS-T2 were close to zero. Our results indicate that CS-B, CS-T, and CS-T2 have substantial genetic variation to allow genetic improvement of female fertility. Some advantages of using CS for genetic

evaluation of sires for female fertility is that it includes fertility performance of both heifer and lactating cows and it takes into account censored records for days open.

Key words: calving success, Holstein, female fertility.

INTRODUCTION

Many studies have reported that female fertility performance has an unfavorable genetic trend in North American Holsteins (e.g. Abdalah and McDaniel, 2000; Lucy, 2001; Van Raden et al., 2004). Thus, a national genetic evaluation of Holstein sires for daughter pregnancy rate (DPR) was implemented in United States (Van Raden et al., 2004). DPR is the predicted merit of sires based on a repeatability animal model after using days open (DO) as an independent variable followed by a transformation of scale.

An unbiased genetic analysis of DO may include fertility records from cows that did not calve in a subsequent parity (Van Raden, personal communication, 2004). Survival analysis and linear models adapted for analysis of censored data were recently proposed to estimate sire's breeding values for days open in dairy cattle (Gonzales-Recio et al., 2006). Both types of analyses gave similar sire rankings, but a linear model adapted for analysis of censored data was found to be easier to implement for the magnitude and scope of a national genetic evaluation program for DO (Gonzales-Recio et al., 2006). In a censored modeling approach, data missing for the trait of inference are replaced by using imputation (Urioste et al., 2007b) or data augmentation (Gonzales-Recio et al., 2006; Urioste et al., 2007b) methodology on the same trait.

Recently, a bivariate linear-threshold approach was used to account for censored data in the analysis of a reproductive trait in beef cattle (Urioste et al., 2007b). Application of this

approach assumes that one trait follows an underlying continuous distribution and that it can be analyzed by using a linear model e.g., calving date, and that it is censored by a correlated categorical trait (e.g. calving success: 1=success; and 2=failure). This approach was applied by Arnason (1999) for genetic evaluation of racing horses and described by Foulley (2004) for mixed model analysis. The idea of using a similar two-trait analysis to account for censored records of DO by using calving success as a correlated trait was proposed by Misztal (personal communication, 2007) and developed by Huang et al.(2007). Conceptually, CS is a female fertility trait that accounts for conception and maintenance of pregnancy for both heifers and lactating cows. Further knowledge about the kind and amount of genetic variation associated with CS by parity in dairy cattle is warranted.

The objective of this study was to estimate heritability and genetic correlation for calving success as a binary or three-category trait by multiple parity animal model analysis in dairy cattle.

MATERIALS AND METHODS

Data

Data in this study were from cows enrolled in a long-term sire selection project designed to explain the genetic change in protein and fat yield in daughters of sires selected for either high or average PTA-fat plus protein yield. There were two concurrent lines: daughters of sires with high (HFP) or average (AFP) genetic merit for fat plus protein yield. Cows from both lines were raised together at the Ankeny dairy breeding research farm at Iowa State University (ISU). All cows were fed and managed as one herd, thus environmental differences between lines were limited. All replacement heifers were born at the farm. Herd

composition was managed to be about 60% HFP and 40% AFP cows in each two lines, respectively.

Three new sires were selected for each selection line every year from the official list of US active AI bulls. Sires were used in two consecutive years to maintain an overlap between new and old sires in every contemporary group. Sires were mated randomly within line. As a result, 96 sires belonging to 16 generation groups were used in this research and each sire had on average 8 daughters.

Data were collected at the Ankeny dairy research farm at Iowa State University from 1986 to 2004. Reproductive performances of 1236 females were used in the analysis of calving success for heifers and lactating cows from their first to fifth parity.

Pedigree of heifers which had first breeding were traced back for at least three generations, resulting in a total of 2184 individuals in the pedigree file. The pedigree file was renumbered by using RENUMF90 v1.7 (Misztal, 2005).

Calving success

The data base for the long-term selection experiment contained extensive recording of information about each breeding-calving event. Up to 61 specific reasons explain why cows were culled from the herd. We began by defining CS_x as a three category outcome ($CS-T_x$) at parity "x" (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve). Every breeding-calving event was assigned scores following the rules given in Table 1. Choice of three categories of $CS-T_x$ was intended to give partial ($CS-T=2$) or no credit ($CS-T=3$) to cows depending on their reproductive history for every breeding-calving event. Scores for $CS-T_x$ accounted for censoring in two ways; for specific reproductive

failure (CS-T=2) versus censoring for all other reasons (CS-T=3). Later we combined scores

of CS-T=1, 2&3 to analyze CS-B$_x$ as a two categorical variable (1=success and 2=failure). A

SAS program was written to assign CS-T$_x$ scores to each breeding-calving event at parity "x"

following the rules of Table 1. Finally, a second definition of CS as a three category trait was

defined by reversing category 2 and 3 of CS-T$_x$, named CS-T2$_x$ (1=success, 2=failure

without opportunity to calve, and 3= failure with opportunity to calve). The CS-T2$_x$

definition was intended to order categories from the best to worst status regarding calving

success performance.

Table 1. Rules for assigning scores to calving success defined as a three-category trait.

Category	Definition	Rule
1	Success to calve	If a cow has conceived and calved
2	Failure with opportunity to calve	- If a cow was culled for infertility. - If a cow died or was culled for non reproductive reasons and one of the following conditions was observed: • If the interval from conception to date leaving herd (CONL) was greater than 280 d (Gestation length). • If CONL was missing and the interval from first breeding to date leaving herd (FBL) was greater than 189 d*. • If FBL was missing and the interval from last calving to date leaving herd (PCL) was greater than 90 d*.
3	Failure without opportunity	The remaining cows. This category includes cows that were alive at the end point of data collection.

* 90 and 189 d were about 90th percentile for PCL and FBL, respectively.

Statistical analysis

Genetic parameters for CS-B, CS-T and CS-T2 were estimated by using a multiple trait

threshold-liability animal model for heifers and lactating cows. The model for the analysis of

either CS-B$_x$, CS-T$_x$ or CS-T2$_x$ was:

$$\mathbf{y}^* = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2ys} + \mathbf{e} \qquad [1]$$

where $\mathbf{y}^*$ = a vector of liabilities for CS-B$_x$ (1=success and 2=failure) or CS-T$_x$ (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) or CS-T2$_x$ (1=success, 2=failure without opportunity to calve, and 3= failure with opportunity to calve); $\mathbf{b}$ = a vector of fixed effects: line of sire selection (AFP or HFP), age at first breeding (mo) for heifers (5 levels for parity 0) and age at calving (mo) for cows (11, 16, 17, 23 and 18 levels for parity 1 to 5, respectively); $\mathbf{a}$ = a vector of random additive genetic effects (2184 levels); $\mathbf{ys}$= a vector of uncorrelated random effects for year-season at first breeding (66 levels for parity 0) and year-season at calving for each parity (63,56, 46, 34 and 23 levels for parity 1 to 5, respectively); $\mathbf{e}$ = a vector of random residual effects; $\mathbf{X, Z_1}$ and $\mathbf{Z_2}$ = incidence matrices relating observations to fixed, random additive genetic and uncorrelated random year-season effects, respectively. The $E\begin{bmatrix} a \\ ys \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$ and $V\begin{bmatrix} a \\ ys \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ 0 & YS & 0 \\ 0 & 0 & R \end{bmatrix}$ where E and V are the expectation and variance operators, respectively. Matrix G= A$\otimes$G$_0$, where A is the numerator relationship matrix of additive genetic effects, and G$_0$ is a matrix (nxn) of additive genetic (co)variances. YS= I$\otimes$ YS_0 and R= I$\otimes$R$_0$, where I is an identity matrix, YS$_0$ and R$_0$ are matrices (nxn) of (co)variances between year-season and residual effects for the n traits, respectively. σ_e^2 was set to 1, and the threshold for CS-B was set to 0; the first and second threshold for CS-T were set to 0 and 1, respectively; Cov(a,ys), Cov(a,e) and Cov(ys,e) were assumed to be zero.

A series of five multiple trait threshold animal models were fit to analyze either CS-B$_x$, CS-T$_x$ or CS-T2$_x$ using parity in successive increments from 0 to 5 to defined traits. The models were 2-t (parity 0 and 1), 3-t (parity 0,1, and 2), 4-t (parity 0,1,2, and 3), 5-t(parity

0,1,2,3, and 4), and 6-t(parity 0,1,2,3,4 and 5). Residual covariance and year-season

covariance among parities were assumed to be zero. The variance components of the

multiple-trait threshold animal model were obtained by Gibbs sampling implemented in

THRGIBBS1F90 (Tsuruta and Misztal, 2006).

POSTGIBBSSF90 and a visual inspection of trace plots for a chain of 200,000 samples

was used to determine the burn-in length, number of samples and thinning ratio. A degree of

belief of number of traits plus two was assigned to the starting values of variance

components. For all analyses a chain of 200,000 samples was run, with a burn-in of 20,000

samples, keeping every 1,000th sample. The saved samples were used to obtain the posterior

mean and posterior standard deviation of variance components, heritability, and genetic

correlation.

Narrow sense heritability (h^2) and genetic correlation from each selected sample were

estimated in all models by $h^2 = \dfrac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_{ys}^2 + \sigma_e^2\right)}$ [2] and $r_g = \dfrac{\sigma_{xy}}{\left(\sigma_x * \sigma_y\right)}$ [3], where σ_a^2 is the

additive genetic variance, σ_{ys}^2 is the year-season variance and, σ_e^2 is one, σ_{xy} is the additive

genetic covariance, σ_x and σ_y are the additive genetic standard deviation of trait x and y,

respectively.

RESULTS AND DISCUSSION

Descriptive analysis

The overall calving success was 69% (Table 2). The incidence of cows which succeed to

calve (CS-B=1) tended to decreased with parity regardless of selection line. This trend

however, was relatively similar from parity 0 to 4 for the two lines. Heifers showed better

fertility than lactating cows, which is in agreement with previous reports of female fertility in

dairy cattle (Dematawewa and Berger, 1998; Jamrozik et al., 2005). Moreover, the

percentage of cows that failed to calve increased with age.

The overall percentage of scores CS-T= 2 (failure to calve with opportunity) and CS-T=3

(failure to calve without opportunity) were 11% and 20%, respectively (Table 2). The

percentage of heifers that failed to calve with (CS-T=2) or without opportunity (CS-T=3)

were nearly similar in each line. However, the percentage of failure with opportunity for

lactating cows was nearly one half the percentage of failure without opportunity in most

parity groups. No differences between lines were observed for the distribution of calving

success defined either as CS-B or CS-T.

Table 2. Number and percentage of cows for calving success as a binary (CS-B) and a three-category (CS-T) trait by line and parity.

Line	Parity	N	CS-B[a] (%)		CS-T[b] (%)		
			1	2	1	2	3
AFP	0	526	85	15	85	7	8
	1	448	67	33	67	8	25
	2	299	67	33	67	10	23
	3	201	58	42	58	16	26
	4	117	51	49	51	16	33
	5	59	25	75	25	24	51
	Total	1650	69	31	69	10	21
HFP	0	710	85	15	85	9	6
	1	601	67	33	67	9	24
	2	400	66	34	66	13	21
	3	265	62	38	62	14	24
	4	165	50	50	50	18	32
	5	82	38	62	38	22	40
	Total	2223	69	31	69	11	20
Overall		3873	69	31	69	11	20

[a]CS-B categories are 1=success and 2=failure,
[b]CS-T categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.

A total of 961 out of 1236 cows left the herd during the experiment. The percentage of cows that left the herd due to sale for reproductive problems was about 27%, whereas the percentage of cows that left the herd due to being sold for reasons other than reproductive problems was 50% and because of death was 23%. Cows that were sold for reproductive problems had a score of CS-T=2 for their last calving record, indicating that they were bred but unable to conceive and maintain pregnancy due to reproductive impairment. Others reported that disposal for reproductive problem was the primary reason (20% of culled cows) for culling in dairy herds (Bascom and Young, 1998).

Logarithm of the marginal posterior density

Tables 3 gives the logarithm of the marginal posterior density of the data (log(p)) for all multiple trait models. The -2*log(p) values were used to compare CS-B, CS-T and CS-T2 models which had the same number of traits. Any CS-B$_x$ multiple trait model fit the data better than its corresponding CS-T$_x$ or CS-T2$_x$ multiple trait model.

Table 3. Logarithm of the marginal posterior density (log(p)) for 5 multiple trait models of calving success as a binary (CS-B) and a three-category trait (CS-T).

Model	Traits	# p	CS-B -2*log(p)	CS-T -2*log(p)	CS-T2 -2*log(p)
2-t	CS_0,CS_1	7	1903395.58	1953452.34	1947592.30
3-t	CS_0,CS_1, CS_2	12	2752460.44	2764554.04	2835307.54
4-t	CS_0,CS_1, CS_2, CS_3	18	3591288.76	3613679.88	3634012.56
5-t	$CS_0,CS_1, CS_2, CS_3, CS_4$	25	4379787.96	4465390.00	4486665.81
6-t	$CS_0,CS_1, CS_2, CS_3, CS_4, CS_5$	33	5172216.90	5227584.88	5174463.59

#p = number of parameters.
CS_0= Calving success for heifers.
$CS_1, CS_2, CS_3, CS_4, CS_5$ = Calving success at parity 1,2,3,4,5, respectively.

Because CS-T$_x$ and CS-T2$_x$ had three categories, there are two conceptual thresholds between the three categories. The first threshold is set to zero and the second threshold is

estimated as a difference from the first threshold. An estimate of the second threshold is automatically part of the solution vector for a threshold model as implemented by THRGIBSS1F90. Estimates of the thresholds within parity are given in Tables 4a and 4b (See values in each column comparing a base trait with addition of successive parities as additional traits). The second thresholds for $CS-T_x$ and $CS-T2_x$ seem to remain nearly constant through different multiple-trait models,which indicates a high degree of stability of thresholds as additional traits were added (Tables 4a and 4b).

Table 4a. Estimates of the second threshold for calving success as a three-category trait (CS-T_x) for five multiple trait models.[a]

Model	$CS-T_0$	$CS-T_1$	$CS-T_2$	$CS-T_3$	$CS-T_4$	$CS-T_5$
2-t	0.95	0.38				
3-t	0.95	0.37	0.55			
4-t	1.04	0.37	0.53	0.63		
5-t	0.99	0.37	0.53	0.64	0.73	
6-t	1.05	0.37	0.55	0.60	0.73	1.19

[a]First threshold was set to be zero.
$CS-T_x$ has the following categories 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
$CS-T_0$= Calving success for heifers, $CS-T_1$, $CS-T_2$, $CS-T_3$, $CS-T_4$, $CS-T_5$ = Calving success at parity 1,2,3,4, and 5, respectively.

Table 4b. Estimates of the second threshold for calving success as a three-category trait (CS-$T2_x$) for five multiple trait models.[a]

Model	$CS-T2_0$	$CS-T2_1$	$CS-T2_2$	$CS-T2_3$	$CS-T2_4$	$CS-T2_5$
2-t	0.45	1.08				
3-t	0.47	1.05	1.01			
4-t	NR	NR	NR	NR		
5-t	0.47	1.06	1.01	1.07	1.38	
6-t	0.47	1.05	1.04	1.08	1.32	2.19

[a]First threshold was set to be zero.
$CS-T2_X$ has the following categories 1=success, 2=failure without opportunity to calve, and 3= failure with opportunity to calve.
$CS-T2_0$= Calving success for heifers, $CS-T2_1$, $CS-T2_2$, $CS-T2_3$, $CS-T2_4$, $CS-T2_5$= Calving success at parity 1,2,3,4, and 5, respectively.
NR= Not reported.

Heritability and genetic correlations

Table 5a gives the posterior means of heritability estimates for CS-B_x, and CS-T_x using different multiple trait threshold animal models. Each column shows the change of the posterior means of heritability for CS-B_x and CS-T_x at a given parity when a trait was added. In general, posterior means of heritability for CS-B_x ranged from low to moderate. From model 6-t, posterior means of heritability for CS-B_x were 0.16(.08), 0.08(.03), 0.23(.07), 0.23(0.07), 0.24(.08) and 0.17(.08) for parity 0 to 5, respectively. Also, posterior means of heritability for CS-T_x ranged from low to moderate. From model 6-t, posterior means of heritability estimates for CS-T_x were 0.17(.08), 0.10(.03), 0.21(.06), 0.22(.07), 0.28(.08) and 0.21(.08) for parity 0 to 5, respectively. The differences between posterior mean of heritability between CS-B_x and CS-T_x were small in all models and parities.

Table 5b gives the posterior means of heritability estimates for CS-B_x, and CS-$T2_x$ using different multiple trait threshold animal models. Each column shows the change of the posterior means of heritability for CS-B_x and CS-$T2_x$ at a given parity when a trait is added. Posterior means of heritability for CS-$T2_x$ ranged from low to moderate values. From model 6-t, posterior means of heritability estimates for CS-$T2_x$ were 0.10(.07), 0.09(.04), 0.29(.09), 0.27(.08), 0.24(.08) and 0.30(.09) for parity 0 to 5, respectively. The differences between posterior means of heritability between CS-B_x and CS-$T2_x$ were small in all models, but model 6-t for parity 5.

The lowest posterior means of heritability on the liability scale for CS-B_x , CS-T_x and CS-$T2_x$ were found for heifers and first-parity lactating cows. This result indicates that year-season accounted for a larger fraction of the phenotypic variance fraction at earlier parities than at later parities, because the residual variance was set to one for all parity groups.

Table 5a. Posterior mean (s.d.) of heritability for calving success as a binary trait (CS-B$_x$) and a three-category trait (CS-T$_x$) for 5 multiple trait threshold animal models.[a]

Model	CS-B$_0$/ CS-T$_0$	CS-B$_1$/ CS-T$_1$	CS-B$_2$/ CS-T$_2$	CS-B$_3$/ CS-T$_3$	CS-B$_4$/ CS-T$_4$	CS-B$_5$/ CS-T$_5$
2-t	0.08 (.07) 0.11 (.07) +.03[b]	0.10 (.05) 0.11 (.05) +.01[b]				
3-t	0.11(.06) 0.12(.05) +.01[b]	0.10(.05) 0.11(.05) +.01[b]	0.26(.08) 0.24(.07) -.02[b]			
4-t	0.16(.05) 0.18(.05) +.02[b]	0.12(.06) 0.13(.05) +.01[b]	0.24(.07) 0.22(.06) -.02[b]	0.23(.07) 0.22(.06) -.01[b]		
5-t	0.11(.05) 0.14(.06) +.03[b]	0.09(.05) 0.10(.04) +.01[b]	0.28(.07) 0.24(.06) -.04[b]	0.23(.08) 0.22(.07) -.01[b]	0.26(.08) 0.29(.08) +.03[b]	
6-t	0.16(.08) 0.17(.08) +.01[b]	0.08(.03) 0.10(.03) +.02[b]	0.23(.07) 0.21(.06) -.02[b]	0.23(.07) 0.22(.07) -.01[b]	0.24 (.08) 0.28 (.08) +.04[b]	0.17(.08) 0.21(.08) +.03[b]

[a]Residual and year season covariance among traits were set to zero.
[b]Difference (CS-T$_x$-CS-B$_x$).
CS-B$_0$= Calving success for heifers, CS-B$_1$,CS-B$_2$,CS-B$_3$, CS-B$_4$, CS-B$_5$ = Calving success at parity 1,2,3,4, and 5, respectively.
CS-T$_0$= Calving success for heifers, CS-T$_1$, CS-T$_2$, CS-T$_3$, CS-T$_4$, CS-T$_5$ = Calving success at parity 1,2,3,4, and 5, respectively.

Table 6a gives posterior means of genetic correlation estimates for subsequent parities for CS-B$_x$ and CS-T$_x$ obtained using different multiple trait threshold animal models. Posterior means of genetic correlations between adjacent parities for CS-B$_x$ and CS-T$_x$ were variable in sign and magnitude across models.

Table 5b. Posterior mean (s.d.) of heritability for calving success as a binary trait (CS-B_x) and a three-category trait (CS-T2$_x$) for 5 multiple trait threshold animal models.[a]

Model	CS-B_0/ CS-T2$_0$	CS-B_1/ CS-T2$_1$	CS-B_2/ CS-T2$_2$	CS-B_3/ CS-T2$_3$	CS-B_4/ CS-T2$_4$	CS-B_5/ CS-T2$_5$
2-t	0.08 (.07)	0.10 (.05)				
	0.09 (.07)	0.10 (.05)				
	+.01[b]	+.00[b]				
3-t	0.11(.06)	0.10(.05)	0.26(.08)			
	0.12(.06)	0.10(.05)	0.28(.09)			
	+.01[b]	+.00[b]	+.02[b]			
4-t	0.16(.05)	0.12(.06)	0.24(.07)	0.23(.07)		
	0.17(.06)	0.11(.05)	0.26(.07)	0.27(.08)		
	+.01[b]	-.01[b]	+.02[b]	+.04[b]		
5-t	0.11(.05)	0.09(.05)	0.28(.07)	0.23(.08)	0.26(.08)	
	0.13(.05)	0.12(.06)	0.27(.08)	0.25(.08)	0.25(.08)	
	+.02[b]	+.03[b]	-.01[b]	+.02[b]	-.01[b]	
6-t	0.16(.08)	0.08(.03)	0.23(.07)	0.23(.07)	0.24 (.08)	0.17(.08)
	0.10(.07)	0.09(.04)	0.29(.09)	0.27(.08)	0.24 (.08)	0.30(.09)
	-.06[b]	+.01[b]	+.06[b]	+.04[b]	+.00[b]	+.13[b]

[a]Residual and year season covariance among traits were set to zero.
[b]Difference (CS-T2$_x$-CS-B_x).
CS-B_0= Calving success for heifers, CS-B_1,CS-B_2,CS-B_3, CS-B_4, CS-B_5 = Calving success at parity 1,2,3,4, and 5, respectively.
CS-T2$_0$= Calving success for heifers, CS-T2$_1$, CS-T2$_2$, CS-T2$_3$, CS-T2$_4$, CS-T2$_5$ = Calving success at parity 1,2,3,4, and 5,respectively.

Table 6b gives posterior means of genetic correlation estimates for subsequent parities for CS-B_x and CS-T2$_x$ obtained using different multiple trait threshold animal models. Posterior means of genetic correlations between adjacent parities for CS-B_x and CS-T2$_x$ were variable in sign and magnitude across models.

Table 6a. Posterior mean (s.d.) of genetic correlation estimates for calving success as a binary trait (CS-B_x) and a three-category trait (CS-T_x) for five multiple trait threshold animal models.[a]

Traits		2-t	3-t	4-t	5-t	6-t
CS-B_0	CS-B_1	0.03(.65)	0.01(.46)	0.07(.31)	-0.49(.27)	-0.04(.32)
CS-T_0	CS-T_1	-0.07(.58)	-0.03(.42)	-0.10(.30)	-0.47(.24)	-0.03(.31)
		-0.10[b]	-0.04[b]	-0.17[b]	+0.02[b]	+0.01[b]
CS-B_1	CS-B_2	--	-0.12(.37)	-0.14(.32)	0.06(.35)	0.50(.23)
CS-T_1	CS-T_2	--	-0.05(.34)	0.14(.31)	0.13(.30)	0.47(.20)
			+.07[b]	+0.28[b]	+0.07[b]	-0.03[b]
CS-B_2	CS-B_3	--	--	0.04(.34)	0.28(.31)	0.20(.31)
CS-T_2	CS-T_3	--	--	-0.16(.30)	0.13(.30)	0.08(.29)
				-0.20[b]	-0.15[b]	-0.12[b]
CS-B_3	CS-B_4	--	--	--	0.14(.26)	0.07(.30)
CS-T_3	CS-T_4	--	--	--	0.28(.23)	0.23(.27)
					+0.14[b]	+0.16[b]
CS-B_4	CS-B_5	--	--	--	--	-0.22(.28)
CS-T_4	CS-T_5	--	--	--	--	-0.34(.26)
						-0.12[b]

[a] Residual and year season covariance among traits were set to zero.
[b] Difference CS-T_x – CS-B_x.
CS-B_0= Calving success for heifers, CS-B_1, CS-B_2, CS-B_3, CS-B_4, CS-B_4 = Calving success at parity 1,2,3,4, and 5, respectively.
CS-T_0= Calving success for heifers, CS-T_1, CS-T_2, CS-T_3, CS-T_4, CS-T_5 = Calving success at parity 1,2,3,4, and 5, respectively.

For CS-B_x, CS-T_x, and CS-T2$_x$ the posterior means of genetic correlations between calving opportunity at parity 0 and parity 1, were close to zero in most multiple trait models (Table 6a and 6b). Therefore, the inclusion of heifer fertility performance adds information to estimates of genetic variance of calving success. Many researchers suggest that fertility in heifers and lactating cows may be treated as different traits, and both have to be used to select for female fertility (Jamrozik et al., 2005).

Table 6b. Posterior mean (s.d.) of genetic correlation estimates for calving success as a binary trait (CS-B_x) and a three-category trait (CS-$T2_x$) for five multiple trait threshold animal models.[a]

Traits		2-t	3-t	4-t	5-t	6-t
CS-B_0	CS-B_1	0.03(.65)	0.01(.46)	0.07(.31)	-0.49(.27)	-0.04(.32)
CS-$T2_0$	CS-$T2_1$	0.12(.64)	0.37(.40)	0.29(.33)	-0.07(.35)	-0.20(.37)
		+0.09[b]	+0.36[b]	+0.22[b]	+0.42[b]	-0.16[b]
CS-B_1	CS-B_2	--	-0.12(.37)	-0.14(.32)	0.06(.35)	0.50(.23)
CS-$T2_1$	CS-$T2_2$	--	-0.08(.34)	-0.15(.33)	0.11(.34)	-0.07(.32)
			+.04[b]	-0.01[b]	+0.05[b]	-0.57[b]
CS-B_2	CS-B_3	--	--	0.04(.34)	0.28(.31)	0.20(.31)
CS-$T2_2$	CS-$T2_3$	--	--	0.22(.33)	0.25(.30)	0.44(.26)
				+0.18[b]	-0.03[b]	+0.24[b]
CS-B_3	CS-B_4	--	--	--	0.14(.26)	0.07(.30)
CS-$T2_3$	CS-$T2_4$	--	--	--	0.06(.31)	0.16(.30)
					-0.08[b]	+0.09[b]
CS-B_4	CS-B_5	--	--	--	--	-0.22(.28)
CS-$T2_4$	CS-$T2_5$	--	--	--	--	-0.03(.28)
						+0.19[b]

[a] Residual and year season covariance among traits were set to zero.
[b] Difference CS-$T2_x$ – CS-B_x.
CS-B_0= Calving success for heifers, CS-B_1, CS-B_2, CS-B_3, CS-B_4, CS-B_5 = Calving success at parity 1,2,3,4, and 5, respectively.
CS-T_0= Calving success for heifers, CS-$T2_1$, CS-$T2_2$, CS-$T2_3$, CS-$T2_4$, CS-$T2_5$ = Calving success at parity 1,2,3,4, and 5, respectively.

General Discussion

Calving success (CS) is a compound trait that indicates cow's ability to conceive, to maintain pregnancy, and to succeed at calving. CS has been used as a measure of female fertility in beef cattle (Meyer et al., 1990; Johnston and Bunter, 1996; Mercandante et al., 2003; Donoghue et al., 2004; Urioste et al., 2007a,b). Some researchers reported moderate heritability for CS (Urioste et al., 2007a,b; and Rust and Groeneveld, 2002) whereas others reported low heritability for CS (Meyer et al., 1990; Johnston and Bunter, 1996; Mercandante et al., 2003; Donoghue et al., 2004; Van der Westhuizen et al., 2001).

In this study, heifers showed higher incidence of calving success than lactating cows. Lactating cows are usually in negative energy balance (NEB) during the early lactation period (Lucy, 2001) when resumption of breeding for next lactation begins. NEB was associated with delayed resumption of ovarian activity, and increased disease susceptibility (Coffey et al., 2003). Therefore, the extent and duration of NEB accompanied by low body condition score may result in poor fertility performance in lactating cows (Lucy, 2001; Rodriguez-Martinez et al., 2008). Also, lactating cows showed a declining trend for calving success as parity increased. This undesirable trend may be a consequence of the aging process and cumulative stress for milk yield across successive lactations (Jansen et al., 1987; Dematatewewa and Berger, 1998).

Small differences between lines were observed for the distribution of calving success defined either as $CS\text{-}B_x$, $CS\text{-}T_x$, or $CS\text{-}T2_x$. This result is in agreement with our previous finding for no differences in days open between lines in Chapter 2.

The outcome of the breeding-calving event depends on both female and male fertility (Lucy, 2001; Rodriguez-Martinez et al., 2008). A cow must be able to produce fertile eggs, recognize fertilization, and further develop the embryo into a viable calf, whereas a bull must be able to produce high quality spermatozoa capable of completing fertilization on insemination. The effect of service sire was not accounted for in this study, because sires were chosen at random at each insemination event within selection lines.

This study is the first documentation of genetic variation of calving success in dairy cattle. Either $CS\text{-}B_x$ or $CS\text{-}T_x$ or $CS\text{-}T2_x$ have substantial genetic variation to allow genetic improvement of female fertility in dairy cattle. However, the posterior mean of heritability for $CS\text{-}B_x$ for all parities was slightly lower than $CS\text{-}T_x$ or $CS\text{-}T2_x$. Others (Urioste et al,

2007b) found heritability estimates for calving success as a binary trait in beef cattle ranging from 0.37 to 0.42 using similar software, a linear-threshold animal model, and the same residual covariance assumptions. Lower heritability estimates for CS found in our study may be attributed to differences in breed and management practices.

A few studies in beef cattle have reported genetic correlations between CS-B records from different parities (Urioste, 2007a,b). In one study genetic correlations were moderate to high but highly variable, and genetic correlations for adjacent parities were negative (Urioste, et al., 2007a). Elsewhere, genetic correlations between CS-B from different parities were positive but highly variable (Urioste, et al., 2007b). Estimates of genetic correlation in this study for CS_2-CS_3 and CS_3-CS_4 were positive but highly variable, which agrees with estimates of genetic correlations reported for Angus cattle (Urioste et al., 2007b).

In order to avoid an extreme category problem in a threshold model analysis for CS-B$_x$ or CS-T$_x$ or CS-T2$_x$, year-season effect was assumed to be an uncorrelated random effect. In order to compare the results of this study with the joint analysis of days open (Reported in Chapter 4), it was necessary to maintain consistent assumptions about the residual covariance among all traits in each successive model, i.e the covariance between residual effects across parities, the covariance between random residual and year-season effects for all parities were zero. The impact of these assumptions about the model on our results are unknown, but similar assumptions were made by other researchers studying the joint analysis of days to calving and calving success in beef cattle (Urioste et al., 2007b).

CS-T will potentially avoid bias for accounting for censored records, but it is difficult to find a methodology to allow for perfect discrimination among cows which terminate their reproductive life due to fertility problems from cows which had censored records for other

unspecified reasons subjected to involuntary culling. A comprehensive recording system for fertility traits and culling like the data available for this research will be required to implement CS-T across farms in a regional or national evaluation. Despite the fact that CS-B did not allow separate reasons for cow culling, it is easy to code. Further research is needed to compare CS-B versus CS-T using field data.

On the other hand, traits like longevity in dairy cattle as stayability (Van Vleck, 1980; Van Doormaal et al., 1985) and functional lactation survival (Jairath et al., 1998) are based on survival status within a cow's lifetime to a fixed endpoint. Stayability (STY) is the survival status at certain fixed ages, eg. 36, 48, 60, 72 and 84 months of total life (Van Vleck, 1980; Hudson and Van Vleck, 1981) or 17, 30, 43, and 55 mo of productive life (Van Doormaal et al., 1985), whereas functional lactation survival (FLS) is the survival status at given lactation eg. first, second, and third lactation (Jairath et al., 1998). Both STY and FLS are defined as a binary trait (1=if cow survived to the specific time, 0=if cow did not survived). Also, CS can be viewed as an indirect measure of survival, because cows which did not calved at a given parity were culled. However, CS may not be the same trait as STY or FLS in dairy cattle.

CONCLUSIONS

This research identifies substantial genetic variation for both CS-B and two definitions of CS-T. The magnitude of genetic variation is large enough to allow these measures of female fertility to be used for genetic improvement. Some advantages of using CS for genetic evaluation of sires for female fertility are that it includes fertility performance of both heifer and lactating cows and it may take into account censored records for day open. Despite the

fact that CS-B did not allow separate reasons for cow culling, it is easy to code. However, further research is needed to compare CS-B versus CS-T in an expanded setting.

REFERENCES

Abdallah, J. M., and T. B. McDaniel. 2000. Genetic parameters and trends of milk, fat, days open, and body weight after calving in North Carolina experimental herds. J. Dairy Sci. 83:1364-1370.

Arnason, T. 1999. Genetic evaluation of Swedish standard-bred trotters for racing performance traits and racing status. J. Anim. Breed. Genet. 116:387-398.

Bascom, S. S., and A.J. Young. 1998. A summary of the reasons why farmers cull cows. J. Dairy Sci. 81:2299-2305.

Coffey, M. P., G. Simm, W. G. Hill, and S. Brotherstone. 2003. Genetic control of energy balance and its relationship to health, fertility and survival of dairy cattle. Proc. of the national dairy genetics workshop in honor of Dr. Ben McDaniel, pp.37-44. Raleigh, NC, USA.

Dematawewa, C. M. B., and P. J. Berger. 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins. J. Dairy Sci. 81:2700–2709.

Donaghue, K. A., R. Rekaya, J. K. Bertrand, and I. Misztal. 2004. Threshold linear analysis of measures of fertility in artificial insemination data and days to calving in beef cattle. J. Anim. Sci. 82:987-993.

Foulley, J. L. 2004. Prediction of random effects in linear mixed models under stochastic censoring. Proc. of stat. in Health Sciences. June 2004, 23-25. Nantes, France.

González-Recio, O. Y., M. Chang, D. Gianola, and K. A. Weigel. 2006. Comparison of models using different censoring scenarios for days open in Spanish Holstein cows. Anim. Sci. 82:233–239.

Huang, C., I. Misztal, S. Tsuruta and T. J. Lawlor. 2007. Methodology of evaluation for female fertility. Interbull Bulletin 37:156-159.

Hudson, G. F. S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64:2246-2250.

Jairath, L., J. C. M. Dekkers, L. R. Schaeffer, Z. Liu, E. B. Burnside, and B. Kolstad, 1998. Genetic evaluation for herd life in Canada. J. Dairy Sci. 81:550-562.

Jamrozik. J., J. Fatehi, G. J. Kistemaker, and L. R. Schaeffer. 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. J. Dairy Sci. 88:2199-2208.

Jansen J., J. Van der Werf, and W. De Boer. 1987. Genetic relationships between fertility traits for dairy cows in different parities. Livest. Prod. Sci. 17:337-349.

Johnston, D. J. and K. L. Bunter. 1996. Days to calving in Angus cattle: Genetics and environmental effects, and covariances with other traits. Livest. Prod. Sci. 45:13-22.

Lucy, M.C. 2001. Reproductive loss in high-producing dairy cattle: where will it end?. J. Dairy Sci. 84: 1277-1293.

Mercandante, M. E. Z., I. U. Packer, A. G. Razook, J. N. S. G. Cyrillo, and L. A. Figueiredo. 2003. Direct and correlated responses to selecting for yearling weight on reproductive performance of Nellore cows. J. Anim. Sci. 81:376-384.

Meyer, K., K. Hammond, P. F. Parnell, M. J. Mackinnon and S. Sivarajasingam. 1990. Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. Livest. Prod. Sci. 25:15-30.

Misztal, I. 2005. Renumf90-renumbering program for BLUPF90 family. Technical note available at: http://nce.ads.uga.edu/~ignacy/numpub/blupf90/docs/Readme.renumf90. Accessed March 3, 2009.

Rodriguez-Martinez, H., J. Hultgren, R. Bage, A. S. Bergqvist, C. Svensson, C. Bergsten, L. Lidfords, S. Gurnasson, B. Algers, U. Emanuelson, B. Berglund, G. Andersson, B. Lindhe, H. Stalhammar, and H. Gustafsson. 2008. Reproductive performance in high-producing dairy cows: Can we sustain it under current practice?. IVIS Reviews in Veterinary Medicine. Available at: http://www.ivis.org/rev/rodriguez/chapter.asp?la=1. Accessed Dec. 1, 2009.

Rust, T. and E. Groeneveld. 2002. Variance component estimation on female fertility traits in two indigenous and two European beef cattle breeds of South Africa. S. Afr. J. Anim. Sci. 32:23-29.

Tsuruta, S., and I. Misztal. 2006. THRGIBBS1F90 for estimation of variance components with threshold-linear models. Commun. 27-31 in Proc. 8th World Congr. Gen. Appl. Livest. Prod. Belo Horizonte, Brazil.

Urioste, J. I., Y. M. Chang, H. Naya, and D. Gianola. 2007a. Genetic variability in calving success in Aberdeen Angus cows under extensive recording. Animal 1:8, pp 1081-1088.

Urioste, J. I., I. Misztal, and J. K. Bertrand.2007b. Fertility traits in spring-calving Aberdeen Angus cattle. 1. Model development and genetic parameters. J. Anim. Sci. 85:2854-2860.

Van der Westhuizen, R. R., S. J. Schoeman, G. F. Jordaan, and J. B. Van Wyk. 2001. Heritability estimates derived from threshold analysis for reproduction and stayability traits in a beef cattle herd. S. Afr. J. Anim. Sci. 31:25-32.

Van Doormaal, B. J., L. R. Schaeffer, and B. W. Kennedy. 1985. Estimation of genetic parameters for stayability in Canadian Holsteins. J. Dairy Sci. 68:1763-1769.

Van Raden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292.

Van Vleck, L.D. 1980. Stayability evaluation as a categorical trait and by considering other traits. J. Dairy Sci. 63:1172-11.

CHAPTER 4. JOINT GENETIC ANALYSIS OF DAYS OPEN AND CALVING SUCCESS IN DAIRY CATTLE USING LINEAR-TRESHOLD ANIMAL MODELS

A paper to be submitted to Journal of Dairy Science

G.A. Gutierrez, M. H. Healey, and P.J. Berger

ABSTRACT

A joint analysis of days open and calving success was implemented to further enhance the identification of cows and sires with greater genetic merit for reproductive performance. The objective of this study was to investigate genetic parameters for days open (DO) and calving success (CS) at different parity groups. CS was defined either as a binary trait (CS-B) or an ordered categorical variable (CS-T). CS-B had two categories (1=success and 2=failure). Two definitions of CS as a three categorical trait were used, CS-T (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) and CS-T2 (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve). Data from 1236 Holstein females from parity 0 to 4 were use to perform a joint analysis of DO and CS with a linear- threshold animal model. Posterior means of heritability for CS-B, CS-T, and CS-T2 were low to moderate. Posterior means of heritability for CS-B from parity 0 to 4 were similar than those for CS-T and CS-T2. Posterior means of CS-B heritability were 0.14(.04), 0.09(.03), 0.28(.07), 0.25(0.06), and 0.26(.06) for parity 0 to 4, respectively, CS-T heritability posterior means were 0.13(.04), 0.09(.03), 0.26(.06), 0.24(0.06), and 0.28(.06) for parity 0 to 4, respectively, and CS-T2 heritability posterior means were 0.15(.04), 0.09(.03), 0.28(.06), 0.26(0.06), and 0.26(.06) for parity 0 to 4, respectively. Posterior means of heritability for DO from joint analysis with CS-B, CS-T and CS-T2 were

similar, and they increased from low to moderate with parity. Posterior means of genetic

correlations between DO and CS in the same parity were positive and varied from low to

moderate, but they had large posterior standard deviations. Calving success is a categorical

trait with similar genetic variation as days open and it is analyzed jointly with days open to

make effective use of the genetic correlation between these two traits in lactating cows. The

joint analysis can identify cows with greater genetic merit for conception at an earlier stage

of lactation and greater success at maintenance of pregnancy.

Key words: days open, calving success, Holstein, female fertility.

INTRODUCTION

Genetic progress for milk yield has increased since 1960 due to the higher selection

intensity for sires and higher reliability of sire's Predicted Transmitting Ability (PTA) from

modern progeny testing schemes (Powell and Norman, 2006). Female fertility, however, has

deteriorated in Holsteins (Abdallah and McDaniel, 2000; Lucy, 2001). An increasing genetic

trend for days open was observed in Holstein cows from North Carolina experimental herds

(Abdallah and McDaniel, 2000) and a declining genetic trend for pregnancy rate was

reported from cows born from 1960 to 1995 for most dairy cattle breeds in US (Van Raden et

al., 2004).

Female fertility is of significant economic importance to dairy producers. Poor female

fertility performance restricts the rate of genetic gain for milk yield, increases insemination

costs, leads to premature culling, and reduces the overall milk yield per cow (Norman et al.,

2009). The marginal cost for additional days open varies from $0.81 to $13.3 and increases

with longer days to conceive (De Vries et al., 2004). Therefore, selection for female fertility will lead to reduced costs at the farm level and to increased longevity in dairy cattle.

Days open (DO) is the most common trait used for genetic evaluation for female fertility in dairy cattle, because it is easy to record at dairy farms (Gonzales-Recio et al., 2006). In addition, a linear transformation of DO has been used for predicting breeding values of daughter pregnancy rate (DPR) in US (Van Raden et al., 2004). The repeatability model is the current statistical method used for genetic evaluation of DO. The main assumption of this model is that the genetic correlation between adjacent parity groups is equal to one and that environmental correlations are similar among parity groups. Such assumptions may not have a biological basis for fertility traits (Jansen et al., 1987), therefore a focused effort to identify a model that can use repeated records, account for censoring, include heifer fertility, and enhance genetic prediction of reproductively sound cows under less constraining assumptions seems warranted.

An unbiased genetic analysis of DO may include fertility records from cows that did not calve in a subsequent parity (Van Raden, personal communication, 2004). Exclusion of records for cows that did not conceive or calve again from data sets would lead to bias in genetic evaluation (Marti and Funk, 2004). The bias will result as reproductive data sets may only contain information from fertile cows and high milk yielding cows (Kadarmideen et al., 2003).

Survival analysis and linear models adapted for analysis of censored data were recently proposed to estimate sire's breeding values for days open in dairy cattle (Gonzales-Recio et al., 2006). Both types of analyses gave similar sire ranking, but a linear model adapted for analysis of censored data was found to be easier to implement for the magnitude and scope of

a national genetic evaluation program for DO (Gonzales-Recio et al., 2006). In a censored

modeling approach, data missing for the trait of inference are replaced by using imputation

(Urioste et al., 2007) or data augmentation methodology on the same trait (Gonzales-Recio et

al., 2006; Urioste et al., 2007).

A bivariate linear-threshold approach was used to account for censored data in the

analysis of a reproductive trait in beef cattle (Urioste et al., 2007) and dairy cattle (Hou et al.,

2009). The concept of including a correlated random variable in a multiple trait setting with a

primary economy trait in animal breeding was first applied by Arnason (1999) for genetic

evaluation of racing horses. Then, Foulley (2004) developed a theoretical framework for the

extension of stochastic censoring models to a mixed model analysis. The idea of using a joint

analysis of calving success and days open was proposed by Misztal (personal

communication, 2007) and developed by others (Huang et al., 2007).

The objective of this study was to estimate genetic parameters for days open and calving

success in different parity groups using a multiple-trait linear-threshold animal model.

MATERIALS AND METHODS

Data

Data in this study were from cows enrolled in a long-term sire selection project designed

to explain the genetic change in fat and protein yield in daughters of sires selected for either

high or average PTA for fat plus protein yield. There were two concurrent lines: daughters

of sires with high (HFP) or average (AFP) genetic merit for PTA milk fat plus protein. Cows

from both lines were raised together at the Ankeny dairy research farm at Iowa State

University (ISU). All cows were fed and managed as one herd, thus environmental

differences between lines were limited. All replacement heifers were born at the farm. Herd composition was managed to be about 60% HFP and 40% AFP.

Three new sires were selected for each selection line every year from the official list of US active AI bulls. Sires were used in two consecutive years to maintain an overlap between new and old sires in every contemporary group. Sires were mated randomly within line. As a result 96 sires belonging to 16 generation groups were used in this research and each sire had on average 8 daughters.

Data were collected at the Ankeny dairy research farm at Iowa State University from 1986 to 2004. Reproductive performances of 1236 females were used in the joint analysis of DO and CS for heifers and lactating cows from their first to fourth parity.

Pedigree of cows which had records was traced back for at least three generations, resulting in a total of 2184 individuals in the pedigree file. The pedigree file was renumbered by using RENUMF90 v1.7 (Misztal, 2005).

Calving success

Calving success was defined either as a binary trait ($CS\text{-}B_x$) or ordered categorical variable ($CS\text{-}T_x$) for each breeding-calving event in parity "x". $CS\text{-}B_x$ had two categories (1=success and 2=failure). Two definitions of CS a three category trait were used, $CS\text{-}T_x$ (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) and $CS\text{-}T2_x$ (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve). Details of the rules to assign $CS\text{-}B_x$, $CS\text{-}T_x$ or $CS\text{-}T2_x$ scores are given in Chapter 3.

CS-T$_x$ was initially designed to take into account of censored records of DO$_x$ in a multiple trait setting. It was expected that CS-T$_x$ would allow one to identify censored records due to fertility impairment (CS-T=2). Choice of three categories of CS-T$_x$ was intended to give partial (CS-T=2) or no credit (CS-T=3) to cows depending on her reproductive history for every breeding-calving event. Scores for CS-T$_x$ accounted for censoring in two ways; for specific reproductive failure (CS-T=2) versus censoring for all other reasons (CS-T=3). The CS-T2$_x$ definition was intended to order categories from the best to worst status regarding calving success performance.

Days open

Days open (DO$_x$) was calculated as the interval from last calving to conception date in parity "x". Conception date was confirmed by pregnancy check at 35 days after the last insemination date. Missing values of DO$_x$ were included in category 2 of CS-B$_x$ or in category 2 and 3 of CS-T$_x$ or CS-T2$_x$. No editing was made for setting upper or lower limits for DO$_x$.

Statistical analysis

Genetic parameters for DO$_x$, CS-B$_x$, CS-T$_x$ and CS-T2$_x$ (x=parity 0 to 4) were estimated by using a multiple trait linear-threshold animal model. Parity was used to define different traits enabling the model to properly account for year-season effects associated with each reproduction event.

The linear model for the multiple-trait analysis of days open was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2ys} + \mathbf{e} \ [1]$$

where $\mathbf{y}$ = a vector of records for days open assumed to be continuously distributed; $\mathbf{b}$ = a vector of fixed effects including: line of sire selection (AFP or HFP), age at calving (mo) of cows as a covariate, year-season at calving for each parity (61,56, 46 and 34 levels of year-four month intervals from 1988 to 2004 for parity 1 to 4, respectively); $\mathbf{a}$ = a vector of random additive genetic animal effects (2184 levels); $\mathbf{e}$ = a vector of random residual effects; and $\mathbf{X}$, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ = incidence matrices relating observations to fixed, random additive genetic, and uncorrelated random year-season effects, respectively. For each DO trait, the Var (a) = $A\sigma_a^2$, and the Var (e) = $I\sigma_e^2$, where A = numerator relationship matrix and I= identity matrix. Residual covariance between different traits, and Cov(a,e) were assumed to be zero.

The model for the analysis of CS-B_x, CS-T_x or CS-$T2_x$ was:

$$\mathbf{y^* = Xb + Z_1 a + Z_2 ys + e} \qquad [2]$$

where $\mathbf{y^*}$ = a vector of liabilities for CS-B_x (1=success and 2=failure) or CS-T_x (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) or CS-$T2_x$ (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve); $\mathbf{b}$ = a vector of fixed effects including: line of sire selection (AFP or HFP), age at first breeding (mo) for heifers (5 levels for parity 0) and age at calving (mo) for cows (11, 16, 17, and 23 levels for parity 1 to 4, respectively); $\mathbf{a}$ = a vector of random additive genetic effects (2184 levels); $\mathbf{ys}$ = a vector of uncorrelated random effects for year-season at first breeding (66 levels for parity 0) and year-season effects at calving for each parity(63,56, 46, and 34 levels for parity 1 to 4, respectively); $\mathbf{e}$ = a vector of random residual effects; $\mathbf{X}$, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ = incidence matrices relating observations to fixed, random additive genetic and uncorrelated random year-season effects, respectively. For each CS trait, Var (a) = $A\sigma_a^2$, Var (ys) = $I\sigma_{ys}^2$,

and the Var (e) = $I\sigma_e^2$, where A = numerator relationship matrix and I= identity matrix. σ_e^2 was set to 1, and threshold for CS-B_x were set to 0; the first and second threshold for CS-T_x or CS-$T2_x$ were set to 0 and 1, respectively. Cov(a,ys), Cov(a,e), Cov(e,e') and Cov(ys,e) were assumed to be zero.

A nine-trait linear-threshold model was fit to jointly analyze CS (CS-B_x, CS-T_x or CS-$T2_x$) and DO_x (x= parity 0, 1,2,3 and 4). The traits were CS_0, CS_1, DO_1, CS_2, DO_2, CS_3, DO_3, CS_4, and DO_4. Residual covariances and year-season covariances among parities were assumed to be zero.

The variance components of the multiple-trait linear-threshold animal model were estimated by Gibbs sampling implemented in THRGIBBS1F90 (Tsuruta and Misztal, 2006). POSTGIBBSSF90 and a visual inspection of trace plots for a chain of 200,000 samples was used to determine the burn-in length, number of samples and thinning ratio. A degree of belief of 11 (number of traits plus two) was assigned to the starting values of variance components. For all analyses a chain of 200,000 samples was run, with a burn-in of 20,000 samples, keeping every 1,000th sample. The saved samples were used to obtain the posterior mean and posterior standard deviation of variance components, heritability, and genetic correlation.

Narrow sense heritability (h^2) for CS and genetic correlation from each selected sample were estimated by $h^2 = \dfrac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_{ys}^2 + \sigma_e^2\right)}$ [3] and $r_g = \dfrac{\sigma_{xy}}{\left(\sigma_x * \sigma_y\right)}$ [4], where σ_a^2 is the additive genetic variance, σ_{ys}^2 is the year-season variance and, σ_e^2 is one, σ_{xy} is the additive genetic covariance, σ_x and σ_y are the additive genetic standard deviation of trait x and y, respectively. σ_{ys}^2 was omitted in the calculation of h^2 for DO.

RESULTS AND DISCUSSION

Descriptive analysis

Table 1 gives the distribution of scores for $CS\text{-}B_x$ and $CS\text{-}T_x$ by parity. The incidence of

calving success was relatively consistent across parity groups in both CS-B and CS-T.

Further discussion about the pattern of the distribution of CS categories by parity was made

in Chapter 3.

Table 2 gives the variation of DO mean and its standard deviation across parity. The mean

of DO tended to increase with parity, but its standard deviation remained almost constant.

Other authors found a similar trends for DO and its standard deviation with parity (Berger et

al., 1981, Norman et al., 2009). An overall mean of 146 d and standard deviation of 88 d for

days to last breeding were reported for non-synchronized cows (Norman et al., 2009). In

addition, an overall mean of 148 d and standard deviation of 89 d for days to last breeding

were reported for Holstein cows breed in 2006 in the Midwest region (Norman et al., 2009).

Table 1. Number and percentage of cows for calving success defined as a binary (CS) and three-category (CS-T) by parity.

Parity	N	CS-B[a] (%)		CS-T[b] (%)		
		1	2	1	2	3
0	1236	85	15	85	8	7
1	1049	66	34	66	9	25
2	699	67	33	67	11	22
3	466	60	40	60	15	25
4	282	50	50	50	17	33
Total	3732	71	29	71	10	19

[a]CS-B scores are 1=success and 2=failure,
[b]CS-T scores are 1=success, 2= failure with opportunity to calve,
 and 3=failure without opportunity to calve.

Table 2. Number of cows, days open mean (s.d.), and age at calving mean (s.d.) by parity.

Parity	N	Days open	Age at calving (mo)
1	766	144.2(88.2)	25.1(2.2)
2	528	149.7(83.4)	38.6(3.4)
3	322	158.3(85.3)	52.3(4.5)
4	169	152.5(84.4)	65.2(5.3)
Total	1785	149.2(86.0)	37.8(13.8)

One clear advantage of adding CS as a trait correlated with DO is the larger effective number of records for CS than the number of records for DO alone; 100%, 37%, 32%, 45%, and 67% in parity 0 to 4, respectively (Tables 1 and 2). This shows that there was a larger pool of cows in the joint analysis than if DO was analyzed as a single trait.

Days open analysis

Table 3 gives posterior means of heritability and genetic correlation estimates for DO_x obtained by multiple trait linear analysis for parities 1 to 4 using Gibbs sampling. Posterior means of heritability for DO_x showed an increasing trend with parity. Posterior mean of heritability for DO_1 was close to those reported from designed experiments (Pryce et al., 1999), but posterior mean of heritability for DO_2, DO_3, and DO_4 were higher than those reported in the literature (Dematawewa and Berger, 1998; Pryce et al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden et al., 2004).

Posterior means of genetic correlations for DO between adjacent parities were positive and moderate. Posterior means of genetic correlation between DO_1 and DO_3 was positive and low, but posterior means of genetic correlations for others pairs of DO_x were positive and moderate. Most multi-parity genetic studies of days open in dairy cattle have used a

repeatability model under the assumption of a genetic correlation of unity between records of

DO_x (Pryce et al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden

et al., 2004). This assumption seems to be unrealistic as we found in this study.

Table 3. Posterior mean (s.d.) of heritability estimates (on-diagonal) and genetic correlations
(off-diagonals) for days open (DO_x) by a four multiple trait linear model.[a]

Trait	Model			
	DO_1	DO_2	DO_3	DO_4
DO_1	0.16(.05)	0.28(.20)	0.06(.20)	0.24(.20)
DO_2		0.20(.05)	0.36(.20)	0.55(.16)
DO_3			0.40(.09)	0.40(.16)
DO_4				0.49(.11)

[a] Residual and year season covariance among traits were set to zero.
DO_1, DO_2, DO_3, DO_4 = Days open at parity 1,2,3,4, respectively.

Joint analysis of days open and calving success

Table 4 gives the logarithm of the marginal posterior density of the data (log(p)) for all

multiple trait linear-threshold animal models. The -2*log(p) values were used to compare

models with the same number of parameters among the joint analysis of DO_x with $CS-B_x$,

$CS-T_x$ and $CS-T2_x$. The joint analysis of DO_x with $CS-B_x$ fitted the data better than

corresponding DO_x-CS-T_x and $DO_x-CS-T2_x$ multiple trait model. The advantage of $CS-B_x$

models over $CS-T_x$ and $CS-T2_x$ models in the joint analysis was also found in the comparison

of $CS-B_x$ over $CS-T_x$ or $CS-T2_x$ model reported in Chapter 3. Also, the joint analysis of

DO_x and $CS-T2_x$ gave a slightly better fit than DO_x and CST_x.

Table 4. Logarithm of the marginal posterior density (log(p) for the joint analysis of days open (DO_x) and calving success as a binary ($CS-B_x$) or three-category trait ($CS-T_x$ and $CS-T2_x$).

Joint analysis	Traits	# p	-2*log(p)
$DO,CS-B_x$	$CS_0, CS_1, DO_1, CS_2, DO_2, CS_3, DO_3, CS_4, DO_4$	59	7336589.07
$DO, CS-T_x$	$CS_0, CS_1, DO_1, CS_2, DO_2, CS_3, DO_3, CS_4, DO_4$	59	7395497.51
$DO, CS-T2_x$	$CS_0, CS_1, DO_1, CS_2, DO_2, CS_3, DO_3, CS_4, DO_4$	59	7392660.73

#p = number of parameters
CS0= Calving success for heifers; CS_1, CS_2, CS_3, CS_4 = Calving success at parity 1,2,3,4, respectively.
DO_1, DO_2, DO_3, DO_4 = Days open at parity 1,2,3,4, respectively.

Heritability and genetic correlations from the joint analysis

Posterior mean of additive genetic variance estimates for DO_x, $CS-B_x$, $CS-T_x$ and $CS-T2_x$

obtained from a set of multiple trait linear-threshold animal models are given in Table 5.

Posterior means of additive genetic variance estimates for CS obtained from the joint

analysis of DO_x and $CS-T_x$ were higher than those obtained from other models. Posterior

means of additive genetic variance estimates for DO obtained from the joint analysis of DO_x

and $CS-T_x$ were higher than those obtained from other models, but parity 1.

Table 5. Posterior mean (s.d.) of additive genetic variance for days open (DO_x) and calving success as a binary ($CS-B_x$) and a three-category trait ($CS-T_x$ and $CS-T2_x$).[a]

Trait	Parity				
	0	1	2	3	4
$CS-B_x$	0.335(.12)	0.153(.05)	0.651(.21)	0.694(.22)	0.879(.26)
$CS-T_x$	0.381(.13)	0.171(.06)	0.644(.19)	0.685(.21)	0.949(.27)
$CS-T2_x$	0.302(.11)	0.125(.04)	0.555(.16)	0.611(.18)	0.715(.20)
$DO_x|CS-B_x$		1572.0(424.8)	1430.7(393.1)	3226.8(791.0)	4428.0(1210.5)
$DO_x|CS-T_x$		1526.2(406.0)	1434.9(392.7)	3265.8(790.06)	4520.1(1229.6)
$DO_x|CS-T2_x$		1591.2(423.3)	1395.5(387.7)	3156.5(781.8)	4374.1(1196.6)

[a] Residual and year season covariances among traits were set to zero.
$CS-B_X$= Calving success (1=success and 2=failure) at parity "x".
$CS-T_X$= Calving success (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) at parity "x".
$CS-T2_X$= Calving success (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve) at parity "x".
DO_x = Days open at parity "x". Parity "x" ranged from 0 to 4.

Posterior mean of heritability estimates for $CS\text{-}B_x$, $CS\text{-}T_x$ and $CS\text{-}T2_x$ are given in Table 6. Similar values of posterior mean of heritability for $CS\text{-}B_x$, $CS\text{-}T_x$, and $CS\text{-}T2_x$ were found in this study. Also, posterior means of heritability for $CS\text{-}B_x$, $CS\text{-}T_x$, and $CS\text{-}T2_x$ varied from low to moderate. In addition, posterior means of heritability for either $CS\text{-}B_x$, $CS\text{-}T_x$ or $CS\text{-}T2_x$ tended to increased with parity. These results are in agreement with CS analysis described in Chapter 3.

The joint analysis of DO_x with $CS\text{-}B_x$ gave similar posterior means of heritability for DO_x than joint analysis of DO_x with $CS\text{-}T_x$ or $CS\text{-}T2_x$ (Table 6). It seems that the posterior mean of heritability for DO_1 was adjusted upward in the joint analysis (Table 6) compared with DO_x analysis (Table 3), but adjusted downward for DO_4.

Table 6. Posterior mean (s.d.) of heritability for days open (DO_x) and calving success as a binary ($CS\text{-}B_x$) and a three-category trait ($CS\text{-}T_x$ and $CS\text{-}T2_x$).[a]

Trait	Parity				
	0	1	2	3	4
$CS\text{-}B_x$	0.14(.04)	0.09(.03)	0.28(.07)	0.25(.06)	0.26(.06)
$CS\text{-}T_x$	0.13(.04)	0.09(.03)	0.26(.06)	0.24(.06)	0.28(.06)
$CS\text{-}T2_x$	0.15(.04)	0.09(.03)	0.28(.06)	0.26(.06)	0.26(.06)
$DO_x|CS\text{-}B_x$		0.21(.05)	0.21(.05)	0.40(.08)	0.43(.09)
$DO_x|CS\text{-}T_x$		0.20(.05)	0.21(.05)	0.40(.08)	0.44(.09)
$DO_x|CS\text{-}T2_x$		0.21(.05)	0.20(.05)	0.39(.08)	0.43(.09)

[a] Residual and year season covariances among traits were set to zero.
$CS\text{-}B_x$ = Calving success (1=success and 2=failure) at parity "x".
$CS\text{-}T_x$ = Calving success (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) at parity "x".
$CS\text{-}T2_x$ = Calving success (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve) at parity "x".
DO_x = Days open at parity "x". Parity "x" ranged from 0 to 4.

Posterior means of heritability estimates for DO_x (Table 6) were larger in the joint analysis than estimates reported in the literature (Dematawewa and Berger, 1998; Pryce et

al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden et al., 2004;

Gonzales-Recio and Alenda, 2005) and those obtained by the random regression procedure

ignoring censoring reported in Chapter 2. The posterior mean of heritability for DO_x ranged

from low to moderate and it increased with parity.

Table 7. Posterior mean (s.d.) of genetic correlation for days open and calving success as a binary trait (CS-B) and a three-category trait (CS-T_x and CS-T2$_x$).[a]

Traits	Days open at parity:			
	1	2	3	4
CS-B$_0$	0.01(.21)	0.47(.18)	0.28(.19)	0.44(.20)
CS-T$_0$	0.04(.20)	0.49(.18)	0.28(.19)	0.46(.20)
CS-T2$_0$	-0.04(.20)	0.43(.19)	0.27(.19)	0.43(.21)
CS-B$_1$	0.17(.20)	0.36(.17)	0.11(.18)	-0.03(.24)
CS-T$_1$	0.11(.19)	0.31(.17)	0.13(.17)	-0.06(.24)
CS-T2$_1$	0.24(.19)	0.39(.16)	0.05(.18)	-0.02(.23)
CS-B$_2$	0.17(.19)	0.28(.17)	0.04(.21)	0.13(.24)
CS-T$_2$	0.15(.18)	0.24(.17)	0.01(.21)	0.15(.24)
CS-T2$_2$	0.18(.18)	0.28(.17)	0.04(.21)	0.08(.23)
CS-B$_3$	-0.15(.21)	0.20(.18)	0.15(.19)	0.11(.22)
CS-T$_3$	-0.09(.20)	0.19(.18)	0.12(.18)	0.08(.23)
CS-T2$_3$	-0.17(.20)	0.21(.18)	0.17(.18)	0.12(.22)
CS-B$_4$	0.02(.19)	0.04(.09)	0.16(.17)	0.04(.20)
CS-T$_4$	-0.09(.19)	0.01(.18)	0.22(.16)	0.01(.20)
CS-T2$_4$	0.11(.19)	0.05(.19)	0.06(.17)	0.06(.19)

[a] Residual and year season covariance were set to zero.
CS-B$_X$= Calving success (1=success and 2=failure) at parity X=0,1,2,3,4, respectively.
CS-T$_X$= Calving success (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) at parity "x".
CS-T2$_X$= Calving success (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve) at parity "x".

Posterior means of genetic correlation estimates by joint analysis for CS-B$_x$- DO_x, CS-T$_x$-

DO_x, and CS-T2$_x$-DO_x are given in Table 7. Genetic correlations between DO_1 and CS-B$_0$,

CS-T$_0$ or CS-T2$_0$ were close to zero. Posterior mean of genetic correlations between DO_x and

$CS-B_x$, $CS-T_x$ or $CS-T2_x$ at the same parity are positive and ranged from low to moderate, but they had large posterior standard deviations. Therefore, cows with lower breeding value for DO will have the genetic potential to succeed in the following parity.

In addition, posterior means of the genetic correlation for DO between adjacent parities were moderate for all joint analysis with CS-B or CS-T (data not shown) and it decreased with parity. Therefore, the repeatability model used in current genetic evaluation of female fertility in US may not be suitable for genetic analysis of DO.

General discussion

Genetic analysis of days open is often difficult, mainly because of unbalanced data and lack of proper methodologies to account for censored records (Chang et al. 2006; Huang et al., 2007). An unbiased multi-parity analysis of DO should include information from cows that do not become pregnant due to fertility impairment, cows that were culled with unknown pregnancy status, and cows without the opportunity to conceive due to the end of data collection.

An alternative approach that allows one to incorporate censored records in the genetic analysis of DO is to use a threshold-linear model which includes a binary trait indicating censoring status and DO (Huang et al., 2007; Hou et al., 2009). Some researchers have investigated the use of CS as a correlated variable with DO in order to account for censored data of DO in Holstein cows. In a simulation study, a linear-threshold model of DO with upper limit of 250 d and CS-B were more accurate in sire variance estimation and heritability of DO than a Cox proportional hazard model, linear DO with records treated as missing, linear DO penalized model at 150, 200, and 250 d (Huang et al., 2007). Elsewhere, a

bivariate threshold-linear model with a binary trait accounting for censored records and DO, showed lower performance in predicting breeding values than a Cox proportional hazard model (Huo et al., 2009).

In Huang et al. (2007), CS-B was treated as a correlated trait accounting only for censored records of DO, which is a similar approach used by Huo et al. (2009). However, the definition of CS used in this study differs from Huang et al.(2007) and Huo et al. (2009) in that it allows one to account for censoring status for both calving success and DO records. Also, CS-T_x and CS-$T2_x$ will allow one to separate censored records due to fertility impairment from other reasons of culling or cow status in the herd. Besides, CS is a female fertility which in addition to DO accounts for maintenance of pregnancy.

CS-B_x,CS-T_x, and CS-$T2_x$ have substantial genetic variation to allow genetic improvement of female fertility in dairy cattle. However, posterior means of additive genetic variance for CS-$T2_x$ were slightly lower than CS-B_x or CS-T_x. Others (Urioste et al., 2007) found heritability estimates for calving success as a binary trait in beef cattle ranging from 0.37 to 0.42 using similar software, linear-threshold animal model and the same residual covariance assumptions. Lower heritability estimates for CS found in our study may be attributed to differences in breed and management practices.

The posterior mean of heritability for DO_x were moderate. Posterior means of heritability for DO_x were larger in the joint analysis than estimates reported in the literature (Dematawewa and Berger, 1998; Pryce et al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden et al., 2004; Gonzales-Recio and Alenda, 2005) and those obtained by the random regression procedure ignoring censoring reported in Chapter 2.

It seems that the posterior means of heritability for DO_1 was adjusted upward, but DO_4 were adjusted downward in the joint analysis compare with DO_x analysis (Table 3).

In order to facilitate convergence and to avoid an extreme category problem in a threshold model analysis for $CS-B_x$, $CS-T_x$ or $CS-T2_x$, the assumptions that correlation between year-season effects for all parities, correlation between residual effects for all parities, and correlation between random residual and a year-season for all parities were zero.The impact of these model assumptions on our results are unknown, but similar assumptions were made by other researchers studying the joint analysis of days to calving and calving success in beef cattle (Urioste, et al., 2007).

CONCLUSIONS

A joint analysis of days open and calving success was implemented to further enhance the identification of cows with greater genetic merit for reproductive performance. DO_x, $CS-B_x$, $CS-T_x$, and $CS-T2_x$ showed low to moderate heritability estimates. It seems that the posterior mean of heritability for DO_1 was adjusted upward, and DO_4 were adjusted downward in the joint analysis. Posterior mean of genetic correlation between DO_x and CS_x at same parity "x" are positive and moderate. The joint analysis can identify cows with greater genetic merit for conception at an earlier stage of lactation and greater success at maintenance of pregnancy. The joint analysis may also enhance the reliability of detecting true genetic differences between cows for fertility because it makes more effective use of all data.

REFERENCES

Abdallah, J. M., and T. B. McDaniel. 2000. Genetic parameters and trends of milk, fat, days open, and body weight after calving in North Carolina experimental herds. J. Dairy Sci. 83:1364-1370.

Arnason, T. 1999. Genetic evaluation of Swedish standard-bred trotters for racing performance traits and racing status. J. Anim. Breed. Genet. 116:387-398.

Berger, P. J., R. D. Shanks, A. E. Freeman, and R. C. Laben. 1981. Genetics aspects of milk yield and reproductive performance. J. Dairy Sci. 64:114-122.

Chang, Y. M., I. M. Andersen-Ranberg, B. Heringstad, D. Gianola, and G. Klemetsdal. 2006. Bivariate analysis of number of services to conception and days open in Norwegian Red using a censored threshold-linear model. J. Dairy Sci. 89:772-778.

Dematawewa, C. M. B., and P. J. Berger. 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins. J. Dairy Sci. 81:2700–2709.

De Vries, A., J. VanLeeuven, and W. Thatcher. 2004. Economic importance of improved reproductive performance. In proceedings 2004 Florida Dairy Reproduction Road Show. pp 33-43.

Foulley, J. L. 2004. Prediction of random effects in linear mixed models under stochastic censoring. Proc. of stat. in Health Sciences. June 2004, 23-25. Nantes, France.

González-Recio, O. and R. Alenda. 2005. Genetic parameters for female fertility traits and a fertility index in Spanish dairy cattle. J. Dairy Sci. 2005 88: 3282-3289.

González-Recio, O. Y., M. Chang, D. Gianola, and K. A. Weigel. 2006. Comparison of models using different censoring scenarios for days open in Spanish Holstein cows. Anim. Sci. 82:233–239.

Hou, Y., P. Madsen, R. Labouriau, Y. Zhang, M. S. Lund, and G. Su. 2009. Genetic analysis of days from calving to first insemination and days open in Danish Holsteins using different models and censoring scenarios. J. Dairy Sci. 92:1229-1239.

Huang, C., I. Misztal, S. Tsuruta and T. J. Lawlor. 2007. Methodology of evaluation for female fertility. Interbull Bulletin 37:156-159.

Jansen J., J. Van der Werf, and W. De Boer. 1987. Genetic relationships between fertility traits for dairy cows in different parities. Livest. Prod. Sci. 17:337-349v.

Kadarmideen, H., R. Thompson, M. Coffey, and M. Kossaibati. 2003. Genetic parameters and evaluations from single- and multiple-trait analysis of dairy cow fertility and milk production. Livest. Prod. Sci. 81:183-195.

Lucy, M. C. 2001. Reproductive loss in high-producing dairy cattle: Where will it end?. J. Dairy Sci. 84: 1277-1293.

Marti, C. F., and D. A. Funk. 1994. Relationship between production and days open at different levels of herd production. J. Dairy Sci. 72:1682-1690.

Misztal, I. 2005. Renumf90-renumbering program for BLUPF90 family. Technical note available at: http://nce.ads.uga.edu/~ignacy/numpub/blupf90/docs/Readme.renumf90. Accessed March 3, 2009.

Norman, H. D., J. R. Wright, S. M. Hubbard, R. H. Miller, and J. L. Hutchison. 2009. Reproductive status of Holstein and Jersey cows in the United States. J. Dairy Sci. 92:3517-3528.

Powell, R. L. and H. D. Norman. 2006. Major advances in genetic evaluation techniques. J. Dairy Sci. 89:1337-1348.

Pryce, J. E., B. L. Nielsen, R. F. Veerkamp, and G. Simm. 1999. Genotype and feeding systems and interactions for health and fertility traits in dairy cattle. Livest. Prod. Sci. 57:193-201.

Tsuruta, S., and I. Misztal. 2006. THRGIBBS1F90 for estimation of variance components with threshold-linear models. Commun. 27-31 in Proc. 8th World Congress Gen. Appl. Livest. Prod. Belo Horizonte, Brazil.

Urioste, J. I., I. Misztal, and J. K. Bertrand. 2007. Fertility traits in spring-calving Aberdeen Angus cattle. 1. Model development and genetic parameters. J. Anim. Sci. 85:2854-2860.

Van Raden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292.

CHAPTER 5. GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

Female fertility is a very complex trait to analyze because its final outcome, a calf, depends on the outcomes of a series of concatenated events related to ovulation, fertilization, embryo survival and fetus survival. Many traits have been used as an indicator of female fertility, but days open (DO) is most frequently used in the literature, because it is easy to record at dairy farms. DO was the choice of base data that are subsequently transformed to calculate daughter pregnancy rate (DPR) for genetic evaluation of female fertility in North American Holstein (Van Raden et al., 2004).

Heritability and repeatability estimates for DO reported in the literature are characteristically low (Dematawewa and Berger, 1998; Pryce et al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden et al., 2004; Gonzales-Recio and Alenda, 2005); meaning that a single record of DO for a cow is not sufficient to predict highly accurate breeding values for DO. Therefore a multi-parity analysis of DO is warranted.

Multi-parity genetic analysis of DO appearing in the literature were completed by using a repeatability animal model (REP) (Dematawewa and Berger, 1998; Pryce et al., 1999; Abdallah and McDaniel, 2000; Kadarmideen et al., 2003; Van Raden et al., 2004; Gonzales-Recio and Alenda, 2005). The basic assumptions of REP are that additive genetic variance is constant through parities and the genetic correlation between subsequent DO records is one. However, one can argue that these assumptions may not have a biological basis.

Chapter 2 gives comparison among a linear random regression animal model (RRM), REP and a multiple trait model (MT) in the estimation of variance components and breeding values for DO. It gives evidence that the additive genetic variance of DO tended to increase with age at calving, although the genetic correlation between adjacent parities were held at unity in order to avoid convergence problems. This result, suggests that inclusion of all records available for each cow will increase the reliability of breeding values for DO. Despite the low heritability of DO there still appeared to be sufficient genetic variation to justify a genetic selection for DO.

The RRM had advantages over the REP model on its ability to predict changes in the additive genetic effects and permanent environmental effects with ages at calving. Also, the RR model takes into account the missing observations for each animal in breeding value prediction, it does not discriminate for the reasons explaining why cows were culled. Involuntary culling was assumed to be the reason for dropouts, however, some cows will leave the herd due to reproductive failure.

An unbiased multi-parity analysis of DO should include information from cows that did not become pregnant due to fertility impairment, cows that were culled with unknown pregnancy status, and cows without the opportunity to conceive due to the end of data collection. An alternative approach to allow one to incorporate censored records in the genetic analysis of DO is to use a threshold-linear model which includes a binary trait indicating censoring status for DO (Huang et al., 2007; Hou et al., 2009).

Chapter 3 introduced the concept of using a similar two-trait analysis to account for censored records of DO by using calving success (CS) as a correlated trait. Also, it introduced CS as an alternative measurement of female fertility. Conceptually, CS is a

female fertility trait that accounts for conception and maintenance of pregnancy for both heifers and lactating cows. CS was defined either as a binary trait (CS-B_x) or ordered categorical variable (CS-T_x) for each breeding-calving event in parity "x". CS-B_x had two categories (1=success and 2=failure). Two definitions of CS as a three category trait were used, CS-T_x (1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve) and CS-$T2_x$ (1=success, 2= failure without opportunity to calve, and 3= failure with opportunity to calve). CS-T_x was designed to take into account of censored records of DO_x in a multiple trait setting. It was expected that CS-T_x would allow one to identify censored records due to fertility impairment (CS-T=2). Choice of three categories of CS-T_x was intended to give partial (CS-T=2) or no credit (CS-T=3) to cows depending on her reproductive history for every breeding-calving event. Scores for CS-T_x accounted for censoring in two ways; for specific reproductive failure (CS-T=2) versus censoring for all other reasons (CS-T=3). The CS-$T2_x$ definition was intended to order categories from the best to worst status regarding calving success performance.

This study is the first documentation for the amount of genetic variation in calving success in dairy cattle. CS-B_x, CS-T_x,and CS-$T2_x$ have substantial genetic variation to allow genetic improvement of female fertility in dairy cattle. However, posterior mean of heritability for CS-B_x for all parities were slightly lower than CS-T_x or CS-$T2_x$. Therefore, there is some latitude to further clarify the desirable properties of one definition over the other.

CS-T and CS-T2 will potentially avoid bias by accounting for censored records, but it is difficult to find a methodology to allow perfect discrimination among cows which terminate their reproductive life strictly due to infertility from other cows which were culled for

unknown –unspecified reasons. A comprehensive recording system for fertility traits and culling will be required to implement CS-T or CS-T2 at farm level. Despite the fact that CS-B did not allow separate reasons for cow culling, it is easy to code.

The definition of CS used in this study differs from Huang et al. (2007) and Huo et al. (2009) in that $CS-B_x$ allows one to account for censoring status for both calving success and DO records. The definition of $CS-T_x$ as a three level ordered categorical trait will allow cows to receive full, partial or no credit for each breeding calving event in her lifetime. Also, the $CS-T2_x$ definition will allow order CS categories from the best to worst status regarding calving success performance. Besides CS is an expression of female fertility which, in addition to DO, accounts for maintenance of pregnancy (embryo and fetus survival).

Chapter four gives the implementation of a joint multi-parity analysis of DO_x and CS_x (x= parity 0 to 4). DO_x, $CS-B_x$, $CS-T_x$, and $CS-T2_x$ showed low to moderate heritability estimates. It seems that the posterior mean of heritability for DO_1 was adjusted upward, and DO_4 were adjusted downward in the joint analysis. Posterior mean of genetic correlation between DO_x and CS_x at same parity "x" were positive and ranged from low to moderate. The joint analysis can identify cows with greater genetic merit for conception at earlier stage of lactation and greater success at maintenance of pregnancy. The joint analysis may also enhance the reliability of detecting true genetic differences among cows for fertility because it makes more effective use of all data.

The data used in this analysis came from a uniquely designed dairy breeding experiment at ISU. This experiment primarily sought to evaluate the effect of sire selection for PTA-fat plus protein yield on milk composition traits. Differences in daughters from sires selected for high and average genetic merit for fat plus protein were found (Berger et al., 2005), but no

differences between lines were found for DO and CS. In another experiment, selection for high genetic merit for fat plus protein resulted in deterioration of female fertility (Pryce et al., 1999). Of course, this does not agree with the result of this study. The reasons for this discrepancy could be attributed to differences in populations, experiment design and environmental factors such as management practices.

The main conclusions are: a) DO and CS have substantial genetic variation to allow genetic improvement by selection; b) Heritability estimates of both DO and CS tend to increase with parity; and c) a joint multi-parity analysis of DO and CS is an alternative approach to account for censored records of female fertility traits with moderate effective heritability.

REFERENCES

Abdallah, J. M., and T. B. McDaniel. 2000. Genetic parameters and trends of milk, fat, days open, and body weight after calving in North Carolina experimental herds. J. Dairy Sci. 83:1364-1370.

Berger, P. J., M. H. Healey, and A. E. Freeman. 2005. Realized difference among daughters of Holstein sires for milk and yield composition after four generations of selection for high and average fat plus protein yield. J. Dairy Sci. 88(Supl. 1):19.

Dematawewa, C. M. B., and P. J. Berger. 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins. J. Dairy Sci. 81:2700–2709.

González-Recio, O. and R. Alenda. 2005. Genetic parameters for female fertility traits and fertility index in Spanish dairy cattle. J. Dairy Sci. 88:3282-3289.

Hou, Y., P. Madsen, R. Labouriau, Y. Zhang, M. S. Lund, and G. Su. 2009. Genetic analysis of days from calving to first insemination and days open in Danish Holsteins using different models and censoring scenarios. J. Dairy Sci. 92:1229-1239.

Huang, C., I. Misztal, S. Tsuruta and T. J. Lawlor. 2007. Methodology of evaluation for female fertility. Interbull Bulletin 37:156-159.

Kadarmideen, H., R. Thompson, M. Coffey, and M. Kossaibati. 2003. Genetic parameters and evaluations from single- and multiple-trait analysis of dairy cow fertility and milk production. Livest. Prod. Sci. 81:183-195.

Pryce, J. E., B. L. Nielsen, R. F. Veerkamp, and G. Simm. 1999. Genotype and feeding systems and interactions for health and fertility traits in dairy cattle. Livest. Prod. Sci. 57:193-201.

Van Raden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292.
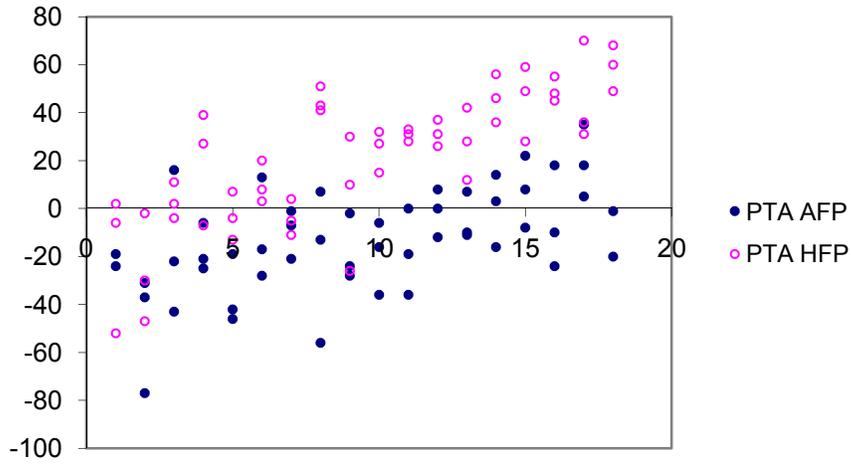
APPENDIX A. ADDITIONAL FIGURES

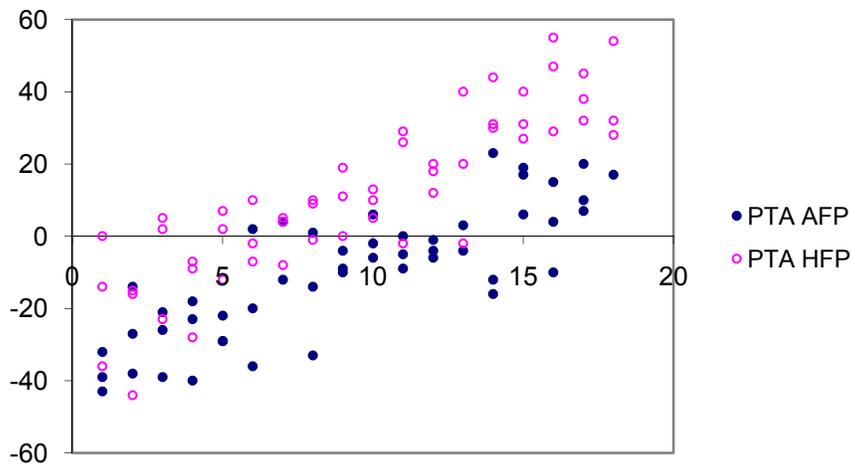Figure 1. Fat yield PTA values of sires by selection lines across sire group.

Figure 2. Protein yield PTA values of sires by selection lines across sire group.
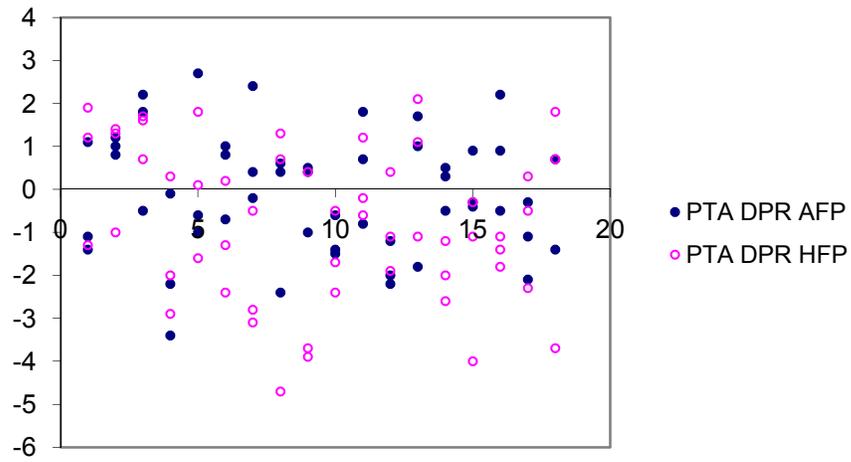
Figure 3. Daughter pregnancy rate (DPR) PTA values o sires by selection lines across sire group.

APPENDIX B. ADDITIONAL TABLES

Table 1. Frequency and percentage of culled cows by primary reason for disposal.

Code	Reason for disposal	Frequency	Percentage
002	Died >72 h, cause unknown	7	0.73
004	Died, self inflicted (broken leg, choked, drowned)	19	1.98
005	Died, respiratory system problem (Hemophilus,etc)	5	0.52
007	Died, digestive system disorder (not scours)	27	2.81
008	Died <=72 h, calving trauma	32	3.33
009	Died, mastitis	20	2.08
010	Died, milk fever or ketosis	6	0.62
011	Died, metabolic disorder – other	9	0.94
012	Died, lymphosarcoma	4	0.42
013	Died, estrus related injury	33	3.43
014	Died, poor health due to advanced age	8	0.83
015	Died, part of sanctioned experiment	1	0.10
150	Bloat	5	0.52
151	Displaced abomasums	8	0.83
152	Fatty liver syndrome	7	0.73
153	Hardware	3	0.31
270	Pneumonia	2	0.21
360	Injury to feet &/or legs	11	1.14
361	Crampy	2	0.21
362	Poor conformation or type of the feet &/or legs	15	1.56
363	Lymphosarcoma	1	0.10
364	Other cancers	5	0.52
365	Injury or trauma to any other area of the cow	11	1.14
480	Disposition	6	0.62
484	Poor health, other (known) reason	17	1.77
485	Poor health, reason unknown	3	0.31
486	Experimental	88	9.16
540	Mastitis, severe	41	4.27
541	Mastitis, chronic	38	3.95
542	Injury to udder/teat	16	1.66
543	Frostbite or frozen teat(s)/udder	12	1.25
544	Blind/dry quarters – long-term condition	6	0.62
545	Slow milk out speed	6	0.62
546	Poor conformation or type of udder &/or teats	33	3.43
630	Freemartin	4	0.42
631	Reproduction - no diagnosed reason	255	26.53
632	Chronic cystic ovaries	3	0.31

Table 1. (continued)

633	Lack of development or poor conf. of repro. tract	11	1.14
634	Persistent metritis or pyometra	7	0.73
635	Embryonic death(s)	15	1.56
636	Abortion(s)	23	2.39
637	Injury or trauma to reproductive tract	21	2.19
638	Other injury/trauma related to dystocia	11	1.14
720	Sold, female, breeding purposes	38	3.95
721	Sold, female, low production	53	5.52
722	Sold, female, no milk letdown	8	0.83
723	Sold, female, low fat &/or protein test	5	0.52
Total		961	100.00

Table 2. Status of cows at the end of data collection by selection line and total.

Status	AFP	HFP	Total
Alive at the end of data collection	109	166	275
Died	88	134	222
Sold for reproductive problems	113	151	264
Sold for other reasons	216	259	475
Total	526	710	1236

Table 3. Status of cows belonging to AFP selection line at the end of data collection by parity.

Status	Parity					
	0	1	2	3	4	5
Alive at the end of data collection	32	32	22	13	5	5
Died	6	20	14	12	22	14
Sold for reproductive problems	25	24	18	21	12	13
Sold for other reasons	15	73	44	38	19	27
Total	78	149	98	84	58	59

Table 4. Status of cows belonging to HFP selection line at the end of data collection by parity.

Status	Parity					
	0	1	2	3	4	5
Alive at the end of data collection	37	53	33	22	13	8
Died	3	41	23	22	18	27
Sold for reproductive problems	44	27	31	20	16	13
Sold for other reasons	25	80	48	36	36	34
Total	109	201	135	100	83	82

Table 5. Cases of assignment of calving success score defined as three category trait.

Case # 1: Cow 3125

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	04/18/89	05/12/89	02/25/90	-	-	-	-	1
1	05/01/90	11/15/90	08/27/91	-	-	-	-	1
2	10/31/91	12/19/91	10/01/92	-	-	-	-	1
3	11/28/92	11/28/92	09/07/93	-	-	-	-	1
4	11/13/93	11/13/93	08/21/94	-	-	-	-	1
5	10/29/94	10/29/94	08/07/95	-	-	-	-	1

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.

Case # 2: Cow 3784

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	01/21/93	01/21/93	10/27/93	-	-	-	-	1
1	01/03/94	05/20/94	02/21/95	-	-	-	-	1
2	06/11/95	10/19/95	07/21/96	-	-	-	-	1
3	09/27/96	09/27/96	07/01/97	-	-	-	-	1
4	09/27/97	10/17/97	07/16/98	-	-	-	-	1
5	10/01/98	11/17/98	08/23/99	-	-	-	-	1

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.

Table 5. (continued)

Case # 3: Cow 3830

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	02/21/93	02/21/93	11/27/93	-	-	-	-	1
1	02/12/94	02/12/94	11/29/94	-	-	-	-	1
2	03/03/95	04/09/95	01/20/96	-	-	-	-	1
3	04/05/96	04/05/96	01/18/97	-	-	-	-	1
4	04/04/97	-	-	08/02/97	196	120	-	2
5	-	-	-	-	-	-	-	-

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
Disposal: Sold; Reason for disposal: Reproduction-no diagnosed reason.

Case # 4: Cow 4773

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	10/12/97	10/17/97	07/22/98	-	-	-	-	1
1	09/24/98	09/24/98	-	07/24/99	367	303	303	2
2	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
CONL>280 d. Disposal: Sold; Reason for disposal: Freemartin.

Table 5. (continued)

Case # 5: Cow 2983

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	08/25/88	02/12/89	11/17/89	-	-	-	-	1
1	03/07/90	03/07/90	12/10/90	-	-	-	-	1
2	02/15/91	07/01/91	04/05/92	-	-	-	-	1
3	-	-	-	08/08/92	125	-	-	2
4	-	-	-	-	-	-	-	.
5	-	-	-	-	-	-	-	.

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
PCL>90d. Disposal: Sold; Reason for disposal: Mastitis, chronic.

Case # 6: Cow 3633

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	02/23/92	02/23/92	11/26/92	-	-	-	-	1
1	01/30/93	04/26/93	02/03/94	-	-	-	-	1
2	04/05/94	04/05/94	01/12/95	-	-	-	-	1
3	03/11/95	04/04/95	-	07/15/95	184	126	102	3
4	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
CONL<280 d. Disposal: Sold; Reason for disposal: Hardware.

Table 5. (continued)

Case # 7: Cow 2977

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	09/12/88	11/17/88	08/10/89	-	-	-	-	1
1	11/02/89	11/02/89	08/02/90	-	-	-	-	1
2	11/20/90	-	-	03/09/91	219	109	-	3

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
FBL<189 d. Disposal: sold; Reason for leaving: injury to udder/teat.

Case # 8: Cow 3096

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	04/19/89	08/26/89	06/01/90	-	-	-	-	1
1	07/27/90	07/27/90	04/30/91	-	-	-	-	1
2	-	-	-	05/09/91	9	-	-	3
3	-	-	-	-	-	-	-	.
4	-	-	-	-	-	-	-	.
5	-	-	-	-	-	-	-	.

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
PCL<90 d. Disposal: Died; Reason for disposal: Died, digestive system disorder.

Table 5. (continued)

Case # 9: Cow 3059

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	12/27/88	06/30/89	03/31/90					1
1	05/26/90	05/26/90	12/03/90					1
2	02/03/91	02/03/91	10/13/91					1
3	-	-	-	11/30/91	48	-	-	3
4	-	-	-	-	-	-	-	.
5	-	-	-	-	-	-	-	.

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
PCL<90 d. Disposal: Died; Reason for disposal: Died, digestive system disorder.

Case # 10: Cow 5883

Parity	Date				PCL	FBL	CONL	CS
	First breeding	Conception	Calving	Leaving				
0	02/28/03	03/04/03	12/09/03	-	-	-	-	1
1	02/08/04	02/08/04	-	NR	-	-	-	3
2	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-
4		-	-	-			-	-
5	-	-	-	-	-	-	-	-

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
Alive at the end of data recording, censored data for calving success.

Table 5. (continued)

Case # 11: Cow 5264

| Parity | Date | | | | PCL | FBL | CONL | CS |
	First breeding	Conception	Calving	Leaving				
0	12/20/99	01/17/00	10/27/00	-	-	-	-	1
1	02/15/01	03/27/01	01/01/02	-	-	-	-	1
2	03/14/02	03/14/02	12/18/02	-	-	-	-	1
3	03/14/03	06/09/03	03/13/04	-	-	-	-	1
4	07/14/04	-	-	NR	-	-	-	3
5	-	-	-	-	-	-	-	-

PCL=interval from last calving to date leaving herd, FBL=interval from first breeding to date leaving herd, and CONL= interval from conception to date leaving herd.
CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.
Alive at the end of data recording, censored data for days open and calving success.

Table 6. Number of calving success records by calving success score and parity.

| Parity | Calving success score (CS) | | |
	1	2	3
1	699	92	258
2	466	79	154
3	282	68	116
4	141	49	92
Total	1588	288	620

CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.

Table 7. Number of days open records by calving success score and parity.

| Parity | Calving success score | | |
	1	2	3
1	699	12	55
2	466	14	48
3	282	11	29
4	141	7	21
Total	1588	44	153

CS categories are 1=success, 2= failure with opportunity to calve, and 3=failure without opportunity to calve.

ACKNOWLEDGMENTS

Many thanks to professors, staff, fellow graduate students and postdoctoral researchers of the animal breeding group at ISU for providing a friendly and good environment to do my academic work.

Finally, my deepest gratitude to my parents and family, who always supported, encouraged and believed in me, in all my endeavors. This dissertation is dedicated to them.