Test-day Models

Breeding value estimation
based on individual test-day records

Marco H. Pool

Test-day Models

Breeding value estimation based on individual test-day records

Marco H. Pool

Test-day Models

Breeding value estimation based on individual test-day records

Promotor: dr. ir. E.W. Brascamp
                Hoogleraar Fokkerij en Toegepaste Genetica
                Wageningen Universiteit

Co-promotor: dr. ir. T.H.E. Meuwissen
                Senior Wetenschapper Genetica en Reproductie
                ID-Lelystad, Instituut voor Dierhouderij en Diergezondheid

Test-day Models

Breeding value estimation based on individual test-day records

Marco Henk Pool

Proefschrift

ter verkrijging van de graad van doctor

op gezag van de rector magnificus

van Wageningen Universiteit,

Dr. Ir. L. Speelman,

in het openbaar te verdedigen

op dinsdag 19 december 2000

des namiddags te half twee in de Aula.

Pool, Marco Henk

Test-day models: Breeding value estimation based on individual test-day records,

Marco Pool – WIAS (Wageningen Institute of Animal Science)
                M.H.Pool@id.wag-ur.nl

Test-day models: Breeding value estimation based on individual test-day records

Pool, Marco Henk

Pool, M. H., 2000. Breeding value estimation based on individual test-day records
This thesis describes choices and decisions made to develop a random regression test-day model. Studies included were performed on Dutch dairy cattle data. Random regression test-day models are preferred above lactation models, because they model both the level and shape of the lactation curve. Single test-day records are used instead of cumulative lactation yields. Therefore, the correction of fixed effects is better and more precise, herd-test-date effects can be accounted for, and if the lactation curve is modeled by a covariance function (i.e., with a random regression function) information from the number, intervals and ordering of test-day records is included. The trend in breeding values for sires was 94 kg of milk per year compared to 106 kg in a repeatability model. Selection in the past was for the level of production and has not influenced the shape of the lactation curve. Correlations between breeding values were high and standard deviations were slightly higher in the test-day model. But for sires with more persistent daughters breeding values seemed to fluctuate less in the random regression test-day model.
For correct modeling of the variance structure higher order functions are needed. A fourth order Legendre polynomials was sufficient for both the genetic and permanent environmental effect. More complete information and a correction for heterogeneity of variance over days in milk allowed a reduction in the least order of fit. However, a multiple-trait random regression test-day model with three parities and a full fit is huge (i.e., 2×15 parameters to be estimated per animal) and probably overparameterized. Therefore, a stepwise-reduced rank procedure was applied, which allowed to half the number of parameter without reducing the goodness of fit considerably. For further extension of the random regression test-day model for the traits milk, fat and protein the stepwise-reduced rank procedure is suggested.

Woord vooraf

Mijn interesse voor het onderzoeken is al jong begonnen. Zo heb ik altijd interesse getoond voor hoe de dingen werken of zijn gemaakt en is ook menig apparaat tot op het laatste schroefje gedemonteerd. In mijn jeugd en tijdens de studie heb ik alle steun en vrijheid gekregen om mijzelf te ontwikkelen in die richting waarvoor ik mij interesseerde. Heit en mem bedankt hier voor. In dat opzicht wil ik ook mijn zus, Reina, en mijn grootouders, pake en beppe noemen. Als boerenzoon groei je op tussen de dieren en heb ik geleerd hoe belangrijk het is om respect en verantwoordelijkheid te tonen voor de dingen die je om je heen ziet, in zowel de natuur als maatschappij.

Mijn interesse voor het wetenschappelijke onderzoek en in het bijzonder het fokkerij-onderzoek is ontstaan tijdens de studie aan de agrarisch hoge school in Leeuwarden. Als stage opdracht heb ik bij KI-NoordWest gewerkt aan de fokwaardeschatting voor gedrag en melksnelheid van koeien tijdens het melken. Deze ervaring was de aanzet om het doorstroom-programma van de studie Veefokkerij aan de Landbouw Universiteit in Wageningen te gaan volgen. In dit verband wil ik Huub Huizinga en Chris Schrooten als begeleiders en mevr. Vollema als lerares veefokkerij noemen.

Mijn interesse tijdens de universitaire opleiding was naar de kant van het onderzoek en in het bijzonder naar de toepassing van de informatica hierin. Tijdens de studie heb ik het vak case-studies als zeer waardevolle ervaren. Samen met Edgar van der Berg en Annet Velthuis hebben we gewerkt aan "De pretentie van persistentie", waarbij we het effect van de weging van deellactaties hebben bestudeerd op de stabiliteit van fokwaarden als er in de loop van de tijd meer productie-gegevens beschikbaar komen (Van Arendonk et al., 1995).

Mijn interesse voor melkvee en onderzoek was reden om te solliciteren op het project: "fokwaardeschatting op basis van individuele proefmelkingen". Oorspronkelijk werd het AIO-project begeleid door Julius van der Werf, maar na zijn vertrek naar Australië is de dagelijkse begeleiding overgenomen door Theo Meuwissen. Theo, ik heb veel bewondering voor je kennis en altijd doeltreffende en toch praktische suggesties en opmerkingen. We waren het niet altijd eens en ik denk dat ik je het ook niet altijd even gemakkelijk heb gemaakt, maar hopelijk ook wel eens heb laten verbazen, bedankt. Ook de leden van de begeleidings-commissie: Gerben de Jong, Johan van Arendonk, Pim Brascamp en Sijne van der Beek wil ik

Contents

General introduction

The objective in breeding is to improve the animal's genotype for the traits of interest (breeding goal). Breeding values are used as a tool for selecting the best animals. Animals with the most favorable genotype are selected to produce the next generation. The offspring of those animals are on average better than the current generation and will upgrade the populations mean for that reason. Selection methods in the past were based on phenotypic comparisons (daughter or daughter-mother comparisons for example), but since the introduction of the procedure of Best Linear Unbiased Prediction [**BLUP**, developed by Henderson (1948)] comparisons became genetically based (i.e., modeling of genetic relationships between animals by including information from relatives). Reliable and accurate estimates of genetic parameters are a prerequisite for animal breeding, namely: to provide correct information about the mechanism of inheritance for the (phenotypically observed) traits under selection; for application in genetic evaluation models to predict breeding values; and in order to design and optimize breeding programs (Van der Werf, 1990). Furthermore, breeding values should be predicted as early as possible to keep the generation interval short, and own performance data should be included as soon as possible (e.g., part lactations) to reduce prediction bias by selection (Danell, 1982).

In the early days, evaluation of dairy cattle in the Netherlands was based on a phenotypically daughter-mother comparison and assumed that all animals produced under equal circumstances. In 1973, a herd-mate comparison, as already applied in the U.S.A. and England, was introduced (Dommerholt, 1979). The herd-mate comparison uses selection index theory, and assumes that cow-effects were not different between groups of offspring from sires; a sire's breeding value was predicted as the regression of its daughter-yield average on the average (sub) population yield. However, the impact of systematic environmental effects like age at calving or season of calving (i.e. fixed effects) had to be known beforehand without error, and breeding values of young bulls were biased downwards because there was no genetic trend correction. In 1981 the procedure of contemporary herd-mate comparison was replaced by a BLUP-procedure (Jansen et al., 1983). Solving the mixed model equations for fixed and random effects jointly gives 'Best Linear Predictions' and including of pedigree information (i.e., accounting for genetic relationships between sires) ensures 'Unbiased' breeding values (Henderson, 1973). The later implies that BLUP takes account of non-random mating of sires and corrects for genetic trends, and further it can handle genetic groups for different sub-populations. Since 1973, when the BLUP procedure became more generally applied, genetic evaluation models have improved a lot. The next step was the introduction of animal models as genetic evaluation models in order to utilize information from the genetic

relationships of sires and dams, and to predict breeding values for both. After all, by accounting for the genetic sire effect only, it was assumed that sires were mated to an average group of dams and that dams were unrelated, which is often not true. However, for large-scale national evaluations only in the beginning of the nineties computer facilities became available to solve the large number of equations for animals in the animal model. Until today, the animal model is still used for the national evaluation of dairy cattle in the Netherlands.

Breeding values of bulls and cows are predicted from 305-day lactation yields. Those 305-day yields are compiled from the individual milk samples which, are taken at 3, 4, or 6 weekly intervals by the official milk-recording system. Individual test-day records are corrected for effects as season, age at calving, herd level and lactation stage on the basis of standard correction factors and standard lactation curves (Dommerholt, 1975; Wilmink, 1987a). To include data as early as possible, running lactations from at least 100 days long are extended to 305-day yields by various regression methods (Wilmink, 1987b). Van Arendonk and Fimland (1983) emphasized that correct averages are needed for adjustment factors of fixed effect classes if extended lactation yields are used for genetic evaluation of dairy cattle. However, by using extended part lactations in the genetic evaluation it seems that predictions of breeding values for sires fluctuate over time if information accumulates. This phenomenon, the so-called RIP-DIP effect (records in progress), occurs in particular for sires with more persistent daughters and for breeding values that are based on many part-lactations. Based on selection index theory it was shown that fluctuations in BLUP breeding values for milk production traits could be reduced by including information in the index about genetic variation in lactation persistency (Van Arendonk et al. 1995).

In the current genetic evaluation model, a lactation model, there is no correction for the effect of herd-test-date, number of test-day records, and interval between test-day records. Also the shape of the lactation curve (i.e. a measure for persistency) is not accounted for, although this may vary between animals. Correct modeling of persistency becomes important when extending part lactations. Using individual test-day records instead of the cumulative lactation yields enables the model to correct on the level of test-day records, and if the shape of the lactation curve is modeled by a random regression function differences between animals in e.g. persistency can be expressed also (Schaeffer and Dekkers, 1994). Further, information about milk yield from the ordering of test-day records, number, and interval between test-day records is included in such a model (Swalve, 1995). The next step, which was studied in this thesis, would be developing the genetic evaluation model from a lactation model into a test-day model (TDM). One reason why the TDM would be better than a lactation model is that the TDM uses single test-day records instead of cumulative lactation yields and therefore can correct better and more precise for fixed effects directly on the level of single test-days.

Compared to lactation models a TDM can account also for the effect of a herd-test-date. For example, if milk recording would have been on a rainy day or after that feed ration had been changed compared to other milk-recordings; the average daily milk yield would have been affected for which a TDM can and a lactation model cannot correct. Another advantage of TDM is that extension of part-lactations beforehand is no longer needed but is done implicitly within the TDM. The fourth and likely most important advantage of TDM is that the model can handle correlations between DIM to be less than one, which allows the TDM to correct for the factor time (i.e., stage of lactation). Therefore, subsequent test-day records are modeled by a lactation function, which assumes that test-day records on different days in milk (DIM) are different but dependent traits with a specific ordering. Modeling the lactation curve with a random regression function and accounting for information from related animals (i.e., adding the genetic relationships matrix) provides the TDM with genetic information about the persistency of a lactation. Thus, based on a TDM a genetic merit lactation curve is predicted for each animal by a range of breeding values. From the genetic merit lactation curve, multiple breeding values can be derived to select for multiple traits of interest such as average daily milk yield or persistency.

The objective of this thesis was to develop the current genetic evaluation model for dairy cattle in the Netherlands further by expanding the present model, from a model based on cumulative lactation yields into a model based on individual test-day records. The aim of the studies described in this thesis was to understand the mechanics of a TDM and to investigate its characteristics with test-day data from Dutch dairy cattle.

Outline of the thesis

In the next five chapters of this thesis, choices and decisions are described for the process of developing a TDM in the Netherlands. The following questions were investigated: which random regression function should be used to describe the lactation curve; what is the goodness of fit of the variance and correlation structure expressed by the TDM; what is the least order of fit necessary for a sufficient accurate fit; and what are the possibilities to reduce the number of parameters to be estimated per animal in order to avoid overparameterization and to reduce the large amount of computer requirements.

Chapter 2 and 3 deal with choosing the correct function to describe the lactation curve within the random regression TDM approach. Chapter 4 describes possibilities to reduce the number of parameters to be estimated per animal in order to reduce the large computing requirements of TDM. Chapter 5 deals with parameter estimation for first parity lactations only. Because memory requirements of deterministic variance component estimation programs based on direct solving of the mixed-model equations are too large, a procedure of Bayesian-inference using Gibbs-sampling was written and implemented to estimate variance

components. Chapter 6 describes how the TDM was extended further into a multi trait lactation TDM for the first three parities. Because of limited computing capacity and in order to get a more parsimonious model, the number of parameters to be estimated per animal had to be reduced further. A stepwise-reduced rank procedure was described and illustrated. In the general discussion (chapter 7) breeding values from a repeatability TDM were compared to breeding values from a higher order TDM.

Prediction of 305-day milk yield
from a limited number of test-days using a test-day model.

(M.H. Pool[a,b], and T.H.E. Meuwissen[b])

[a] Wageningen Institute of Animal Science (WIAS).
[b] Department of Genetics and Reproduction. Institute of Animal Health and Science
(ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

ABSTRACT

Four test-day models were compared for their ability to predict 305-d milk yield production in an experimental farm with weekly milk recording. Individual lactation deviations from the average lactation curve were modeled by a constant (model LEVEL), a straight line (model LINE), a constant before the production peak and a line thereafter (model SPLINE), and Wilminks (1987a) lactation curve (model WILMINK). The LEVEL model had higher residual variance, lower correlations with true average daily milk yields and generally higher mean square error of predicted missing observations than the other models, which yielded very similar results for these statistics. The model LINE was preferred over the models SPLINE and WILMINK, because of its simplicity.

INTRODUCTION

Presently 305-d milk yields are calculated using various regression methods (see e.g. Wilmink, 1987b). A problem with these methods is that they do not account for the effect of an individual test-day on the test-day yield of a cow (Reents and Dopp, 1996). Further the 305-d prediction methods do not account for the individual lactation curves of a cow (Schaeffer and Dekkers, 1994), which may differ mainly due to differences in persistency. The latter effect is expected to cause the RIP-dip effect (records in progress dip) of proven bulls with high persistency and many lactations of second crop daughters in progress.

A test-day model (**TDM**) can account for the test-day effect on individual test-day records and for the persistency of a cow. Currently, EBV's are predicted by first predicting 305-d milk yields from the test-day records and then predicting EBV's from the (predicted) 305-d yields, whereas a TDM predicts directly EBV's from the test-day records. The latter implies that all effects are simultaneously accounted for. With a TDM, it is more natural to predict average daily milk yields of a cow, which is equivalent to 305-d yields, because it equals 305-d milk yield divided by 305.

A TDM should account for the stage of lactation of the cow. Many lactation functions have been described in the literature (Wood, 1968; Schaeffer et al. 1977; Batra et al., 1987; Grossman and Koops, 1988; Elston et al., 1989; Stanton et al, 1992; Sherchand et al., 1995; Gengler, 1996). Here we will fit the average lactation curve by simply fitting a class of DIM effect. This is more flexible than any other standard lactation curves, but it's fit costs more degrees of freedom. However, there are many thousands of test-day records such that some loss of degrees of freedom hardly reduces the accuracy of the predictions.

The deviations of the individual cows from the average lactation curve at different stages of lactation may be described by a simpler curve than a standard lactation curve. This is especially the case when we are only interested in simple statistics such as 305-d milk yield or persistency of the cows. In fact complicated curves require estimation of many parameters, which may be a problem when the number of test-days per cow is small. Loss of degrees of freedom due to many parameters for each cow can result in inaccurate estimation, because there is only a limited number of test-day records per cow. Such inaccurate estimates will hamper accurate prediction of 305-d yields.

The aim of this paper is to predict average daily yields from a limited number of test-days. Alternative TDM will be compared for their predictive ability for several patterns of missing test-day records, such as when only a part of the lactation is known or when the interval between the test-day records is varied. The aim is not to improve the current predictions of 305-d milk yields, but to develop a TDM based method to predict 305-d yields. Such a TDM would be a good base for developing breeding value estimation models for test-day productions.

DATA AND MODELS

The present study is based upon 951 lactations records with weekly measured test-day yields from the experimental farm 't Gen (ID-DLO, The Netherlands). Milk production was measured weekly until cows were at least 150 days in milk. All lactations started between June, 1987 and April, 1996.

The test-day records were analyzed by the following models:

LEVEL: $y_{ij} = \mu + ys + age + kDIM + TD + a_i + e_{ij}$
LINE: $y_{ij} = \mu + ys + age + kDIM + TD + a_i + b_i * DIM + e_{ij}$
SPLINE: $y_{ij} = \mu + ys + age + kDIM + TD + a_i + b_i * DIM^* + e_{ij}$
WILMINK: $y_{ij} = \mu + ys + age + kDIM + TD + a_i + b_i * DIM + c_i * \exp(-0.05*DIM) + e_{ij}$

y_{ij}: j^{th} test-day milk yield in i^{th} lactation (lactations are assumed uncorrelated)

μ: intercept

ys: year-season of calving (3 monthly classes per year)

age: age at calving (4 monthly classes)

kDIM: class of days in milk * parity

         (weekly classes with parity defined as first and later)

DIM: number of days in milk at the test-day

DIM^*: $DIM^* = DIM - 42$ for $DIM \geq 42$; otherwise $DIM^* = 0$

a_i: random effect of the lactation

         (genetic plus within lactation permanent environment effect)

b_i: random regression coefficient on days in milk for i^{th} lactation

c_i: random regression coefficient on the Wilmink (1987b) factor for i^{th} lactation

e_{ij}:   residual

In all four models the average lactation curve is described by the effect of the class of days in milk (weekly classes within first and later parity; kDIM). The a_i, b_i and c_i terms, model the deviation of the individual lactation curve from the average lactation curve expressed by kDIM. The model LEVEL includes only the term a_i, which implies that the deviation from the average lactation curve is assumed to be constant over the whole lactation for each individual lactation. In the model LINE, the deviation from the average lactation curve is expected to be a straight line for each individual lactation, which is modeled by the terms a_i and b_i. The b_i term expresses the individual deviation of the average slope of the average lactation curve and may be interpreted as the persistency of the lactation. In the SPLINE model, the deviation is assumed constant for the first 42 days of lactation (until the peak production), and is assumed to follow a straight line after the peak production, with the slope b_i representing persistency. In the WILMINK model, the deviation from the average lactation curve is expected to follow the Wilmink (1987a) curve: $a_i + b_i * DIM + c_i * \exp(-0.05*DIM)$. The random regression on $\exp(-0.05*DIM)$ for each individual lactation, could model a fast change at the begin of the lactation curve followed by an almost straight line.

REML estimation of variances

Variances and covariances were estimated by the EM-REML algorithm:

$$\sigma_{\alpha\beta} = (\hat{\boldsymbol{\alpha}}_i{}'\hat{\boldsymbol{\beta}}_i + \mathbf{tr}(\mathbf{C}_{\alpha\beta})\sigma_e^2)/\mathbf{q} \qquad \text{and} \qquad \sigma_e^2 = \mathbf{y}'\hat{\mathbf{e}}/(n - \text{rank}(x))$$

where: $\hat{\boldsymbol{\alpha}}_i{}'(\hat{\boldsymbol{\beta}}_i)$:   vector with MME solutions for term $\hat{\boldsymbol{\alpha}}_i{}'(\hat{\boldsymbol{\beta}}_i)$, with $\boldsymbol{\alpha}_i{}'(\boldsymbol{\beta}_i)$ being a_i, b_i or c_i

         $\mathbf{C}_{\alpha\beta}$:   part of the inverse MME which corresponds to the equations for $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$

q: number of effects in α (equals number of effects in ß)
y: data vector
ê: vector with estimated residual terms
n: number of observations
rank(x):   rank of the fixed effect part of the MME

Comparison of models

The goodness of fit of modeling individual deviations from the average lactation curve, for the different models, is investigated by analyzing the complete data set, (i.e. all known weekly test-days records are included), and several subsets, (i.e. part lactations and varied lengths of test-day intervals).

Differences in goodness of fit between the models are expressed by:

1)   the residual variances
2)   correlations between predicted average daily milk yield ($\bar{y}_i$ = 305-d yield / 305,

   i.e., all $\bar{y}_i$ of the sub data sets were correlated to those off the complete data set):

   LEVEL: $\bar{y}_i = a_i$

   LINE: $\bar{y}_i = a_i + b_i * (305/2)$

   SPLINE: $\bar{y}_i = \{42a_i + 263 * (a_i + 131 * b_i)\}/305$

   WILMINK: $\bar{y}_i = \{a_i + b_i * (305/2) + c_i * \int_{1}^{305} \exp(-0.05*DIM)\ dDIM \}/ 305$

3)   the mean square error of predictions of missing observations:

   $$MSEP = \sum (y_i - \hat{y}_i)^2 /n$$

   where y_i :   test-day record that is missing in the sub data set, but
                         known in the complete data set
                $\hat{y}_i$:   predicted value of missing record using the models
                         LEVEL, LINE, SPLINE and WILMINK
                n :   number of missing records in the sub data set

RESULTS
Residual variances

REML estimates of the (co)variances of the terms a_i, b_i and c_i are in Table 1. Including the b_i term in the model LINE reduces the residual variance with 2.8 kg² daily milk yield. The residual variance for the models LINE, SPLINE and WILMINK are almost identical. The

Table 1: REML estimates of variance and covariance for the a_i, b_i and c_i terms from the LEVEL, LINE, SPLINE and WILMINK models (in kg² milk)

Covariance	LEVEL	LINE	SPLINE	WILMINK
a_i,a_i	17.970	21.664	19.619	21.669
a_i,b_i		-0.046	-0.330	-0.047
b_i,b_i		0.001	0.001	0.001
a_i,c_i				-0.004
b_i,c_i				0.000
c_i,c_i				0.000
e_i,e_i	9.398	6.563	6.555	6.563

Table 2: Correlations between predicted average daily milk yield in part lactation sub sets with the complete data set from the LEVEL, LINE, SPLINE and WILMINK models

DIM in sub set[1]	number of records	LEVEL LEVEL*	LEVEL LINE*	LINE LINE*	SPLINE SPLINE*	SPLINE LINE*	WILMINK LINE*
complete	36,288	1.000	.9748	1.000	1.000	.9986	1.000
≤ 147	27,978	.9480	.9067	.9285	.9192	.9226	.9285
≤ 133	27,028	.9372	.8920	.9105	.8997	.9038	.9105
≤ 119	26,068	.9240	.8742	.8940	.8833	.8887	.8940
≤ 105	25,118	.9063	.8504	.8786	.8735	.8806	.8786
≤ 91	24,171	.8829	.8216	.8597	.8634	.8719	.8597
≤ 77	23,222	.8530	.7869	.8335	.8367	.8467	.8335
≤ 63	22,144	.8199	.7498	.8016	.7821	.7925	.8016
≤ 49	21,223	.7746	.7025	.7515	.7049	.7136	.7515
≤ 35	20,281	.7040	.6292	.6557	.6240	.6312	.6557
≤ 21	19,352	.6194	.5444	.5530	.5411	.5469	.5530

[1] Part-lactations are created by taking a specified period of the complete lactation. This is done for only 50% of the animals (randomly chosen) so that all other fixed effects can be estimated.

variance of the a_i and b_i terms are equal for the models LINE and WILMINK which indicates that the regression on the exp(-0.05*DIM) term hardly affects the predictions. According to the residual variances the model SPLINE is slightly better than LINE and WILMINK, which are better than LEVEL.

Correlations between predicted average daily milk yields

The correlation between predicted average daily milk yield in the sub sets for all four models is compared with the predicted average daily milk yield in the completed data set for the model itself and for model LINE. The latter because it was assumed that LINE (or WILMINK) yielded the best prediction of average daily yield in the complete data set. For part-lactations (Table 2) correlations improve with the number of days in milk and are highest for LINE and WILMINK, lower for SPLINE and the lowest for LEVEL. The WILMINK and LINE correlations are equal because of the negligible effect of the c_i term. When the intervals between test-days were varied (Table 3) correlations decreases with the length of the interval, but differences are relative small. As before, the correlations for LINE and WILMINK are equal.

Table 3: Correlations between predicted average daily milk yield in sub sets with varied test-day intervals with the complete data set from the LEVEL, LINE, SPLINE and WILMINK models

milkrec. frequency [1]	number of records	correlations of sub sets with complete data set (indicated by *)					
		LEVEL LEVEL*	LEVEL LINE*	LINE LINE*	SPLINE SPLINE*	SPLINE LINE*	WILMINK LINE*
weekly [2]	36,288	1.000	.9748	1.000	1.000	.9986	1.000
2-weekly	18,120	.9970	.9724	.9957	.9930	.9951	.9957
3-weekly	9,032	.9943	.9678	.9907	.9845	.9903	.9907
4-weekly	7,231	.9881	.9637	.9833	.9759	.9828	.9833
5-weekly	6,057	.9828	.9557	.9766	.9643	.9767	.9766
6-weekly	5,180	.9837	.9566	.9770	.9631	.9773	.9770
7-weekly	4,520	.9753	.9515	.9695	.9552	.9700	.9695
8-weekly	4,042	.9673	.9441	.9619	.9497	.9619	.9619
9-weekly	3,566	.9557	.9280	.9513	.9318	.9510	.9513
10-weekly	3,293	.9585	.9351	.9522	.9314	.9520	.9522

[1]   sub sets are generated by deleting all records for a specific test-day for all animals.

[2]   complete data set, weekly intervals

Mean square error of predictions of missing observations

In order to compare the different models LEVEL, LINE, SPLINE and WILMINK for their predictive ability, mean square errors of prediction of missing observations (MSEP) for different lengths of part lactations are presented in Table 4 and for varied test-day intervals in Table 5. Results show that MSEP is less sensitive for longer between test intervals than for part lactations. The goodness of fit increases when the intervals become shorter and when the length of part lactations becomes longer. This is clear for all four models for varied intervals but less clear for LINE, SPLINE and WILMINK when the length of the part lactation increases from 77 to 133 days, which may be due to a too high weight of the information of the test-days for the prediction of the slope of the line, which then deviates too much from zero. The too high weight may be due to the imperfect model, which becomes mainly apparent in the extrapolation that is needed to predict $\hat{y}_i$.

Table 4: Mean square error of predictions of missing observations in part lactation sub sets from the LEVEL, LINE, SPLINE and WILMINK models

DIM in sub set	number of records	number of pred. records	Mean square error of pred. of missing rec.			
			LEVEL	LINE	SPLINE	WILMINK
complete	36,288					
≤ 147	27,978	8,310	15.78	21.61	22.41	21.61
≤ 133	27,028	9,260	15.83	22.64	23.14	22.64
≤ 119	26,068	10,210	16.01	23.15	22.96	23.15
≤ 105	25,118	11,160	16.51	22.16	20.52	22.16
≤ 91	24,171	12,107	17.30	20.71	17.48	20.71
≤ 77	23,222	13,056	18.27	20.03	16.75	20.03
≤ 63	22,144	14,004	19.21	19.60	17.97	19.60
≤ 49	21,223	14,921	20.57	19.90	20.05	19.90
≤ 35	20,281	15,862	22.39	21.29	21.85	21.29
≤ 21	19,352	16,657	24.48	23.32	23.90	23.32

DISCUSSION AND CONCLUSIONS

Four TDM: LEVEL, LINE, SPLINE and WILMINK were compared for the goodness of fit for average daily milk yield based on weekly milk yield data, recorded in an experimental herd. Differences between the models in goodness of fit were small. The model LINE,

SPLINE and WILMINK had substantially lower residual variances, which suggests that these models should be preferred over LEVEL. The model LINE gave identical results as the model WILMINK, which implies that model LINE should be preferred because of simplicity. The LINE model had higher correlations with "true" average daily milk production, estimated in the complete data set. The only shortcoming of LINE is an improper extrapolation of missing observations. This is probably because polynomials, such as LINE, yield poor predictions of extrapolated records. The poor prediction of extrapolated records may result in larger changes

Table 5:   Mean square error of predictions of missing observations in sub set with varied test-days intervals from the LEVEL, LINE and WILMINK models

Milk recording frequency [1]	number of records	number of pred. rec.	Mean square error of pred. of missing rec.			
			LEVEL	LINE	SPLINE	WILMINK
weekly [2]	36,288					
2-weekly	18,120	8,946	9.64	6.97	6.91	6.97
3-weekly	9,032	11,885	10.17	7.54	7.49	7.54
4-weekly	7,231	13,431	10.07	7.59	7.55	7.59
5-weekly	6,057	14,342	10.38	7.98	7.93	7.98
6-weekly	5,180	14,902	10.40	8.17	8.11	8.17
7-weekly	4,520	15,309	10.70	8.59	8.54	8.59
8-weekly	4,042	15,655	10.81	8.72	8.70	8.72
9-weekly	3,566	15,876	10.96	8.97	8.96	8.97
10-weekly	3,293	16,129	11.15	9.29	9.30	9.29

[1]   sub sets are generated by deleting all records from a test-days for 50% of the animals (randomly chosen) so that all other fixed effects needed to predict the missing records can be estimated.

[2]   complete data set

of $\bar{y}_i$ as the lactation progresses. This was not seen in the correlations (Table 2), but the variances of the predicted $\bar{y}_i$ were higher with LINE than with LEVEL (unpublished results).

In conclusion the model LINE combines simplicity with a high level of goodness of fit of average daily milk yields. It seems therefore to provide a simple and good model from which TDM for breeding value estimation can be developed.

———————

Prediction of daily milk yields
from a limited number of test-days using test-day models.

(M. H. Pool[a,b], and T.H.E. Meuwissen[b])

[a] Wageningen Institute of Animal Science (WIAS).
[b] Department of Genetics and Reproduction. Institute of Animal Health and Science
(ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

ABSTRACT

A data set of weekly milk yield records was used to compare different test-day models for their ability to inter- and extrapolate missing milk yields. The criterion to compare the models were: 1) the (co)variance structure modeled compared with the observed (co)variance structure in the data, and
2) MSEP, which compared the predicted value of a missing record to the known value of the record. The test-day models used were LEG(m), which are Legendre polynomials with an order of fit of m, and EXP, which is an exponential lactation function.

When fitting the LEG(m) models, the criteria 1) and 2) generally improved with an increasing order of fit as expected. The model EXP, which contains three random regression coefficients, was between LEG(1) and LEG(2), which contain two and three coefficients respectively. The improvement of the criteria with m in LEG(m), became negligible after LEG(5). Thus, a 5th order Legendre polynomial yields a good fit, with a minimum number of parameters. Also, the correlation structure of milk yields among days in milk modeled by LEG(5) resembled the correlation structure that was observed in the data. However the modeled variances at the end of lactation were larger than those observed in the data, except when LEG(0) was used. Legendre polynomials with a fit less than five, yielded correlation structures that clearly deviated from the observed correlations, especially in the case of LEG(0). Overall LEG(5) is preferred to use to develop a genetic test-day model for breeding value estimation.

INTRODUCTION

Recently, test-day models (**TDM**) have been suggested for the genetic evaluation of dairy bulls and cows. TDM analyze individual test-day records of cows instead of 305-d milk yields, which are currently used. The main advantages of using TDM for genetic evaluations are: 1) Individual test date effects can be included in the model, which affects the test-day yields substantially (Reents and Dopp, 1996); 2) The number of records per cow, and the interval between records can be accounted for; 3) The number of cows with records at the same test

date exceeds the number of cows that enter a herd-year-season class in a full lactation model, which increases the accuracy of the adjustment for fixed effects, especially in small herds; 4) TDM can account for individual differences in the shape of the lactation curves of cows, which includes the persistency of the lactation (Schaeffer and Dekkers, 1994). The latter reduces the fluctuations of predicted breeding values over time due to differences in persistency, which occur if a relatively large number of incomplete records are added to the evaluation (the records in progress, RIP-dip effect (Jamrozik et al. 1997b).

Ptak and Schaeffer (1993) suggested a repeatability TDM, which assumes that covariances between successive test days are equal to those between test days that are far apart. The application of a multi-trait TDM with all 305 lactation days as different traits relaxes this assumption, however such models are highly over parameterized. In the literature about TDM [see review by Swalve (1995)] three types of models have been suggested to reduce the number of parameters of the multi-trait model: 1) The reduced rank multi-trait model [**RMT**, (Wiggans and Goddard, 1996)] where a canonical transformation is used to reduce the multi-trait analysis to a reduced number of independent single trait analysis; 2) Covariance functions [**CF**, (Kirkpatrick et al., 1994)] where a conceptually infinite number of traits is assumed by modeling the (co)variances between test days with a covariance function, and 3) The random regression model [**RRM**, (Schaeffer and Dekkers, 1994)] where the shape of the lactation curve is modeled by a random regression function.

In the RMT approach the full (co)variance matrix is needed, which requires a large number of cows with records on both days in milk (**DIM**) for every combination of two DIM to estimate genetic parameters. The RRM and CF model are equivalent as shown by Meyer and Hill (1997), and Van der Werf et al. (1998). Any (co)variance structure in the data [Var(**y**), where y is the data vector] can be modeled equally by either a CF model or a RRM. In both the CF and RRM approach Var(y) is modeled by a function, i.e. the covariance function and the random regression function, respectively. The choice of the lactation function to describe the data is an essential and critical element of both the RRM and CF models.

In the literature, many studies were on the fitting of lactation curves [e.g. see review, (Masselin et al. 1987)]. In more recent studies emphasis has been focussed on modeling variability between individual lactation curves instead of curves which can be assigned a form that applies to all cows (Pérochon et al., 1996; Stanton et al., 1992; White and Brotherstone, 1997), where the latest studies described the implementation of different curves in TDM (Guo and Swalve 1997ab; Jamrozik et al., 1997a). Most authors compared the different lactation curves based on criteria as the correlation between observed and predicted yields, mean absolute residuals or the variance and distribution of the residual terms. Jamrozik et al. (1997a) found small practical differences when using the Ali and Schaeffer (1987), and Wilmink lactation curve (Wilmink 1987a) in RRM in all respects, however the function with a

higher number of parameters, the Ali and Schaeffer curve, had a slight advantage. Because of only small differences between different lactation functions, Guo and Swalve (1997a) recommended that it would be worthwhile to exploit those in such a way that simple functions with fewer parameters still have sufficient fit when used in a TDM.

The different TDM could be compared also by maximum likelihood tests, however the significance of these tests depends on the information content of the data. More important for the estimation of breeding values is the accuracy of prediction of the true 305-d milk yields, and the fluctuations of those predictions as information accumulates.

Studies on the inter- and extrapolation of lactation records have been described in literature frequently (Guo and Swalve, 1995; Van Arendonk and Fimland, 1983; Wilmink 1987ab; Woolliams and Waddington, 1998). Recently, VanRaden (1997) described a method of best prediction for interpolation of test-day records to calculate 305-d yields, which was more accurate than the test interval method, but less accurate than the simultaneously equations of BLUP. The latter resembles a TDM and different TDM will be investigated in the current paper for inter- and extrapolation of test-day records.

The aim of this paper was to predict daily milk yields with a TDM, based on different random regression functions. Predictions were based on a data set with weekly records from which observations were deleted according to various patterns. Predictions with deleted observations were compared with predictions without deleted observations, which, because of the high frequency of recording, approximate the true parameter values. Additionally, a comparison of predictions of deleted observations to the actual observations was used to select the best random regression function. The shape of individual lactation curves was modeled phenotypically. An appropriate phenotypic RRM seems a sound base to develop a genetic TDM for breeding value evaluation.

MATERIALS AND METHODS
Data

The data consisted of 951 lactation records (536 first and 415 later parity, from 605 animals) of Holstein Friesian cows from the ID-DLO experimental farm " 't Gen" over the period June '87 to April '96. Milk yields were measured each week according to the regular national milk recording scheme, and each test day is the sum of the evening and next morning milk yield. The data set contained in total 36,288 test-day records, i.e. an average of 38 test days per lactation. Milk production was measured weekly, lactations were at least 150 days long (75% of all lactations were longer than 230 days, 50% were longer than 293 days, and 25% were longer than 301 lactation days), and at maximum 305 days long. The average test-day yield was 27.7 kg milk per day with a standard deviation of 7.6 kg milk per day.

Model

In the RRM approach the shape of the lactation curve of a cow is split into two parts: a general part (the average lactation curve), and an animal specific part (the deviations from that average lactation curve) which can be modeled by a fixed and a random function, respectively. The shape of the average lactation curve, in this study, is described by fitting a class of days in milk effect (weekly classes within first and later parities, **cDIM**). This way of describing the average lactation curve is more flexible than by any standard lactation curve function.

The different RRM that were compared are:

FIXED: $y_{ij} = \mathbf{x_{ij}}'\boldsymbol{\beta} + e_{ij}$
EXP: $y_{ij} = \mathbf{x_{ij}}'\boldsymbol{\beta} + a_i + b_i\, sDIM_{ij} + c_i \exp(-0.05 * DIM_{ij}) + e_{ij}$
LEG(m): $y_{ij} = \mathbf{x_{ij}}'\boldsymbol{\beta} + \boldsymbol{\phi_{ij(m)}}'\, k_{i(m)} + e_{ij}$

Where y_{ij} = test-day milk yield j in animal × lactation i (i.e., lactations of the same cow are assumed independent); $\mathbf{x_{ij}}'$ = incidence row vector for fixed effects $\boldsymbol{\beta}$ of test-day milk yield j in animal × lactation i; $\boldsymbol{\beta}$ = [μ; ys; age; cDIM; TD]' with μ = the overall mean; ys = year season of calving (3 monthly classes within year); age = the age at calving (4 monthly age classes); cDIM = class of DIM × parity (weekly, within first and later parities); and TD = test date (date of milk recording). The number of classes within each fixed effect were 1, 36, 14, 88, and 460 respectively; (s)DIM_{ij} = (standardized) number of DIM at test day j of animal × lactation i (where sDIM = (DIM - 150) / 150); a_i = random effect of the animal × lactation i (which is the genetic plus within lactation permanent environmental effect); b_i = random regression coefficient on sDIM in milk for animal × lactation i; c_i = random regression coefficient on the exponential of -0.05 DIM for animal × lactation i; $\boldsymbol{\phi_{ij(m)}}'$ = row vector of random regression factors of the mth order Legendre polynomial (Kirkpatrick et al., 1990) of $sDIM_{ij}$; and $k_{i(m)}$ = a (m by 1) vector of individual random regression coefficients of animal × lactation i, with m as the order of fit. Legendre polynomials were used here because they are orthogonal and normalized, which results in better converge and more accurate results than with conventional polynomials, i.e., [1, DIM_{ij}, DIM_{ij}^2, etc.].

In matrix notation, the TDM can be written as: $\mathbf{y = X\,\boldsymbol{\beta} + Z\,u + e,}$

where $\mathbf{y}$ = data vector; $\boldsymbol{\beta}$ = vector with fixed effects; $\mathbf{u}$ = [$\mathbf{u_1}$'.. $\mathbf{u_i}$'..]' with $\mathbf{u_i}$ = vector of random regression coefficients of animal × lactation i with $\mathbf{u}_i = k_{i(m)}$ for the models LEG(m), and $\mathbf{u_i}$ = [a_i, b_i, c_i]' for model EXP; $\mathbf{e}$ = vector of residual effects; and $\mathbf{X}$, and $\mathbf{Z}$ the incidence and covariate matrixes.

The variance of **y** is:

$$\text{Var}(\mathbf{y}) = \mathbf{Z} \, \text{Var}(\mathbf{u}) \, \mathbf{Z}' + \text{Var}(\mathbf{e}) = \mathbf{Z} \, (\mathbf{I} \otimes \mathbf{P}) \, \mathbf{Z}' + \mathbf{R} \qquad [1]$$

where **P** = phenotypic covariance matrix of the random regression coefficients, assumed to be the same for all animal × lactations; **I** = identity matrix; **R =** diagonal matrix with the residual variance; i.e., **R** = diag$\{\sigma_e^2\}$, and $\otimes$ = Kronecker product. Furthermore, the model assumed that $E(\mathbf{u}) = 0$, $E(\mathbf{e}) = 0$ and $E(\mathbf{y}) = \mathbf{X} \, \boldsymbol{\beta}$.

The random regression coefficients (a_i, b_i, c_i, and $\boldsymbol{k_{i(m)}}$) model the deviation of the individual lactation curve from the average lactation curve expressed by cDIM. The model FIXED assumed only fixed effects and was used to estimate (co)variances of the residuals of different DIM, without imposing a model on Var(**y**).

Model LEG(0) only included the 0th order polynomial which was a constant. Hence, LEG(0) assumed that the deviation from the average lactation curve was constant over the whole lactation, and $k_{i(0)}$ represented an animal × lactation effect. In the model LEG(1), the 1-th order polynomial was included, which was a straight line. Hence, LEG(1) assumed that the individual deviations from the average lactation curve followed a straight line, which was modeled by the individual level of production (0-th order) and the slope (1-th order). The slope may be interpreted as the persistency of the lactation. In the model EXP, the deviations from the average lactation curve was expected to follow the lactation curve of Cobby and Le Du (1978), which was modified by Wilmink: $a_i + b_i * \text{sDIM} + c_i * \exp(-0.05 * \text{DIM})$ (Wilmink 1987a). The model EXP models for each individual lactation a fast change at the beginning of the lactation by the term $\exp(-0.05 * \text{DIM})$ followed by an almost straight line. The higher order Legendre polynomials (LEG(2) and higher) allowed a more flexible shape of the lactation curve and should be able to model the individual deviations from the average lactation curve more precisely.

The matrix of variances and covariances of a_i, b_i, c_i, $\boldsymbol{k_{i(m)}}$, i.e. **P**, and σ_e^2 were obtained by Henderson's EM-REML algorithm (Henderson, 1984).

Comparison of Models

The goodness of fit of the TDM models was investigated by analyzing the complete data set including all known weekly test-day records and several so called subsets, with part lactations of different lengths or varied intervals between successive test days. Subsets with different lactation lengths were generated by deleting all records after a certain DIM for fifty percent of randomly chosen animals such that all other fixed effects can still be estimated. Subsets with longer intervals between test dates were generated by deleting all records for particular test dates. The records deleted from the complete data set in order to create the subsets will be called missing records in the following.

Table 1. Phenotypic variances of the random regression coefficients and residual variances (σ_e^2) for milk yield (kilograms squared) modeled a test-day model using Legendre polynomials of different orders of fit m [LEG(m)] and an exponential function (EXP) [1].

Model	$k_{0(m)}$ [2]	$k_{1(m)}$	$k_{2(m)}$	$k_{3(m)}$	$k_{4(m)}$	$k_{5(m)}$	$k_{6(m)}$	$k_{7(m)}$	σ_e^2
EXP[3]	0.96	15.14	64.56						5.67
LEG(0)	35.94								9.39
LEG(1)	40.33	8.30							6.56
LEG(2)	37.12	7.54	3.07						5.53
LEG(3)	38.21	6.76	2.70	1.52					4.96
LEG(4)	37.51	6.36	2.52	1.38	0.91				4.61
LEG(5)	36.90	6.24	2.52	1.33	0.85	0.53			4.38
LEG(6)	36.79	6.14	2.51	1.32	0.85	0.58	0.35		4.20
LEG(7)	36.72	6.09	2.53	1.31	0.86	0.58	0.39	0.25	4.07

[1] Covariances between random regression coefficients in the models are not shown but were estimated.

[2] $k_{j(m)}$ = random regression coefficient j in model LEG(m) of order of fit m.

[3] Variance components of the random regression coefficients for the model EXP where $k_{0(m)}$, $k_{1(m)}$ and $k_{2(m)} = a_i$, b_i and c_i, respectively, and are on a different scale than those of LEG(m).

Table 2. Correlations between random regression coefficients modeled by a test-day model using a third and fifth order of fit Legendre polynomial, LEG(3) and LEG(5) respectively.

model		$k_{0(m)}$ [1]	$k_{1(m)}$	$k_{2(m)}$	$k_{3(m)}$	$k_{4(m)}$
LEG(3)	$k_{1(3)}$	0.2879				
	$k_{2(3)}$	-0.1705	0.0119			
	$k_{3(3)}$	0.1705	-0.1040	-0.0740		
LEG(5)	$k_{1(5)}$	0.2291				
	$k_{2(5)}$	-0.2952	-0.0279			
	$k_{3(5)}$	0.1246	-0.1185	-0.1524		
	$k_{4(5)}$	-0.3441	-0.0356	-0.0757	-0.2653	
	$k_{5(5)}$	0.1838	-0.1835	-0.0472	-0.1663	-0.4297

[1] $k_{j(m)}$ = random regression coefficient j in model LEG(m) using Legendre polynomials with an order of fit m.

The different TDM were compared for their overall goodness of fit based on the complete data set and their ability to predict the missing data in the subsets. The following two criteria were used to compare the models:

1. A graphical comparison of the Var(**y**) modeled by the models EXP and LEG(m), where y includes a record at every DIM. Var(**y**) was estimated by Equation [1], which requires the estimated **P** and **R** matrices modeled by the different TDM. The Var(**y**) modeled by the different TDM was compared with the observed (co)variances between the residual terms, which were obtained from the model FIXED.

2. The mean square error of predictions of missing observations (**MSEP**) investigates how good the missing records could be predicted. MSEP was calculated as:

$$\text{MSEP} = \sum_{i=1}^{n}(y_i - \hat{y}_i)^2 / n_i \qquad [2]$$

where y_i is the test-day record that is the i-th missing records which is known in the complete data set; $\hat{y}_i$ is the predicted value of missing record using the models EXP or LEG(m), and n is the number of the missing records in a subset.

RESULTS
(Co)variance Estimates

REML estimates of the phenotypic variances for the random regression coefficients (a_i, b_i, c_i, and $k_{i(m)}$ terms), and residual variances for milk yield, modeled by the different TDM presented in Table 1. Legendre polynomials with an order of fit of eight (LEG(8)) and higher could not be estimated because of convergence problems, probably due to information matrices that were close to singular.

Including the first order polynomial LEG(1) compared with LEG(0) reduced the residual variance for milk yield with 2.8 kg². The residual variance in the model EXP was 0.89 kg² smaller than in the model LEG(1) and somewhat higher than LEG(2). The residual variance for the other models decreased with the number of parameters, i.e. with the order of fit of the Legendre polynomial. Hence, as expected, the model with the highest order had the smallest residual variance, although the differences between the higher order polynomials were small. The correlations estimated between the random regression coefficients (a_i, b_i, c_i, and $k_{i(m)}$ terms) are presented in Table 2. Overall, the correlations were quite small (smaller than 0.43), but not negligible. For higher order random regression coefficients the correlations tended to become stronger (also for LEG(6) and LEG(7), results not shown).
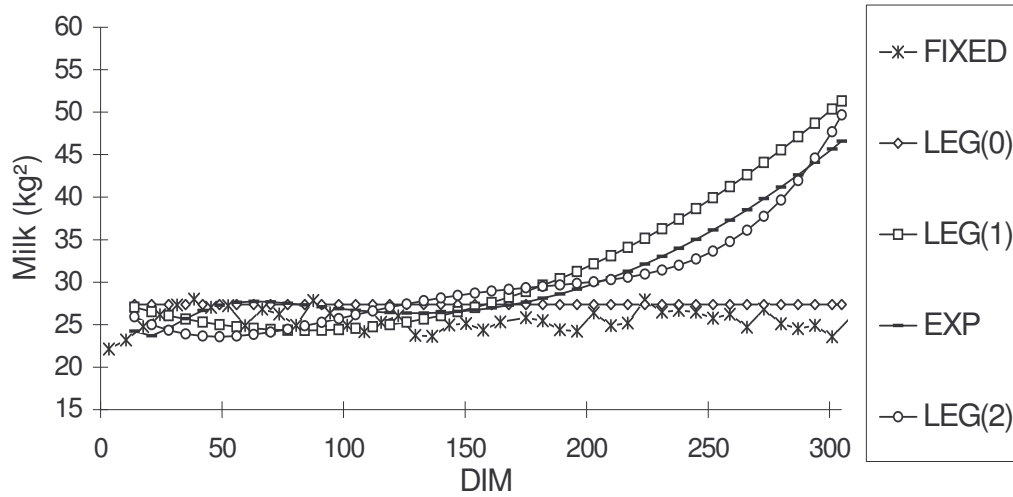
Figure 1. Variances of milk yield over DIM modeled by a test-day model using Legendre polynomials of different orders of fit [LEG(0), LEG(1) and LEG(2)] and an exponential function (EXP), compared with the observed variances between the residual terms, obtained from a model with correction for fixed effects (FIXED).
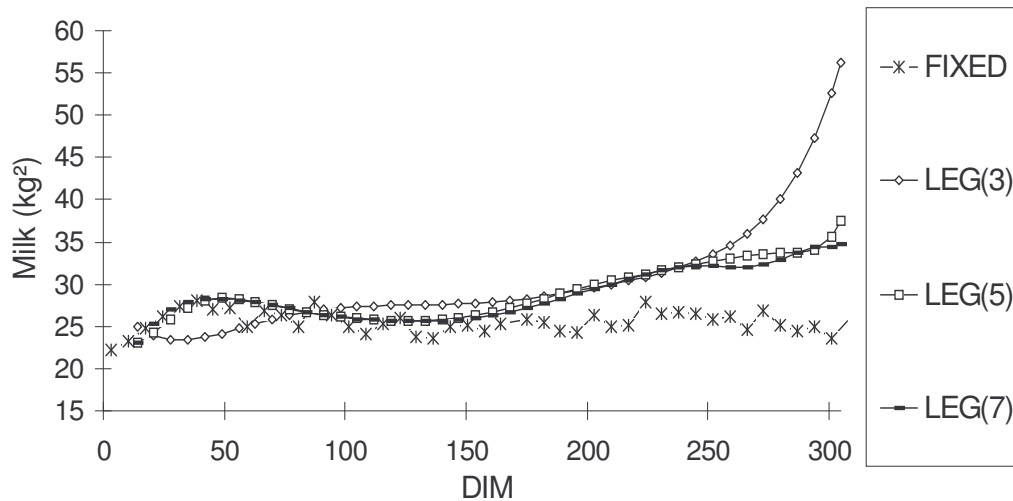

Figure 2: Variances of milk yield over DIM modeled by a test-day model using Legendre polynomials of different orders of fit [LEG(3), LEG(5), and LEG(7)] compared with the observed variances between the residual terms, obtained from a model with correction for the fixed effects (FIXED).

20

Modeled versus Observed (Co)variances

The variance of milk yields at different DIM modeled for each TDM can be calculated from the covariate matrix of the random regression coefficients (a_i, b_i, c_i, and $k_{i(m)}$) and the residual variance. The variance modeled is different for each TDM (Figures 1 and 2) and varied over DIM, except for model LEG(0) where it was constant. Model LEG(1) showed, a quadratic shape of the variances over DIM. Model EXP allowed for a more flexible shape at the beginning of the lactation and had a similar shape as LEG(1) further on in the lactation but the variance modeled at the end of the lactation was lower. The higher order Legendre polynomials showed a more flexible shape and the goodness of fit increased with the order of fit. Differences between LEG(5), LEG(6) (not shown), and LEG(7) were relatively small. The higher order Legendre polynomials seemed to resemble more closely the observed variances of test-day records at various DIM, which were obtained by calculating (co)variances of the residuals from the model FIXED. However, overall the variances of the yields was most accurately modeled by LEG(0).
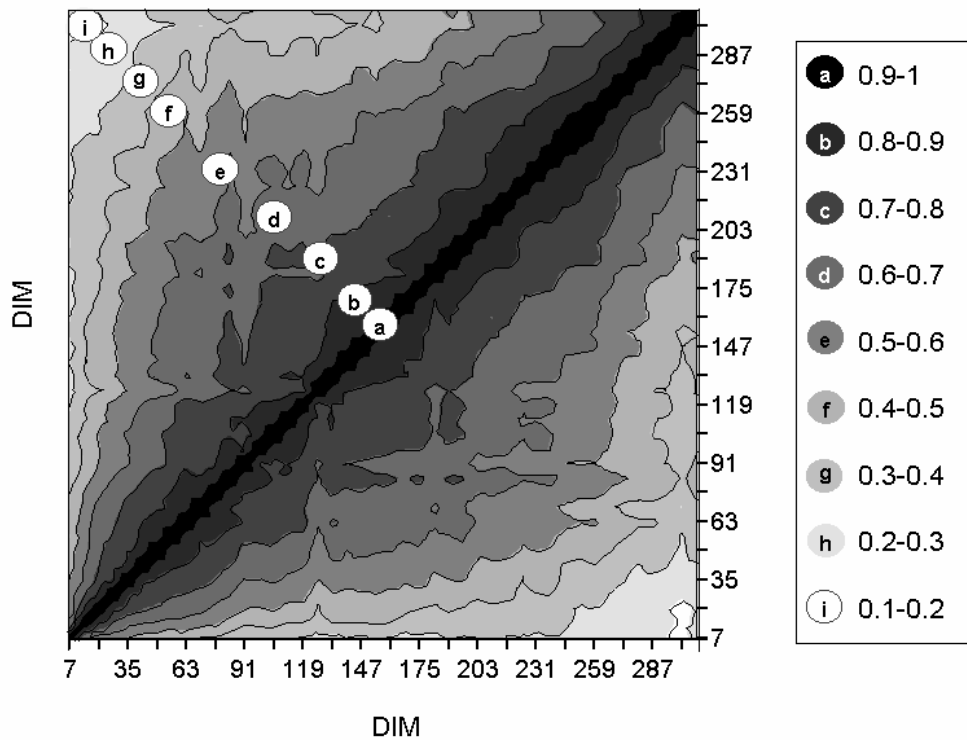
Figure 3.   Observed correlation structure for milk yields among DIM obtained by calculating (co)va-riances of the residuals from a model with correction for the fixed effects (FIXED).
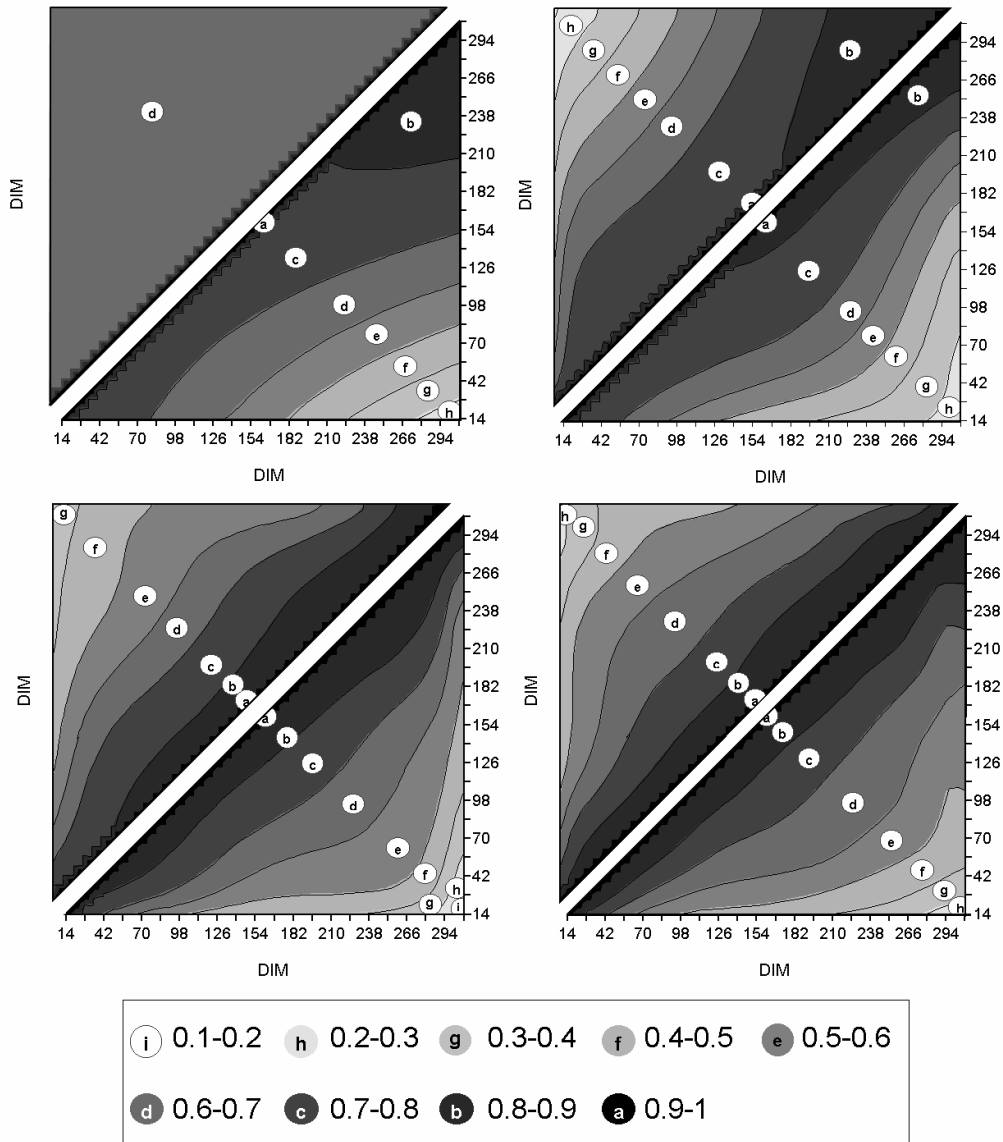
Figure 4. Correlation structure for milk yields among DIM modeled by a test-day model using Legendre polynomials of different orders of fit m [LEG(m)] and an exponential function (EXP). Stacked areas on top, from left to right are: LEG(0) (upper triangle), LEG(1) (lower triangle), EXP (upper triangle) and LEG(2) (lower triangle). Stacked areas on bottom, from left to right are: LEG(3) (upper triangle), LEG(4) (lower triangle), LEG(5) (upper triangle) and LEG(7) (lower triangle).

Figure 3 shows the observed correlation structure of milk yields among DIM realized in the complete data set as a stacked area, which were obtained by calculating (co)variances of the residuals from the model FIXED. The correlation structure modeled by the models EXP, LEG(0) to LEG(5), and LEG(7) are presented as stacked areas in Figure 4. It seemed that a Legendre polynomial with an order of fit of five and higher (Figure 4) most closely resembled the observed correlation structure (Figure 3) and that model LEG(0) yielded the poorest.

Mean Square Error of Predictions of Missing Observations (MSEP)

MSEP for different lengths of part lactations are presented in Figure 5. Generally MSEP de-creased when the length of part lactations became longer, except for the models LEG(1), EXP, and LEG(3). For these models the MSEP increased as the length of the part lactation increased from 77 to 133 days. This unexpected increase may be due to a too high weight on the information of the test days used for the prediction of the slope of the line, which then deviates too much from zero. The higher order Legendre polynomials (LEG(5) and higher) did not show this increase, meaning that a higher order of fit was necessary in order to get good predictions when using information from part lactations.

Figure 5. Mean square error of predictions of missing observations from a test-day model using Legendre polynomials of different orders of fit [LEG(m)] and an exponential function (EXP) for subsets with different part lactation lengths.

The MSEP for varied test-day intervals is presented in Figure 6. Results showed that MSEP slightly increased with the length of intervals between test days, however, the differences were small relative to the MSEP for different part lactation lengths. Model LEG(0) showed the poorest results for the interpolation of yields (Fig. 6). Extrapolation of yields by

model LEG(0) was better than for LEG(1) and EXP (Fig. 5), but was inferior to that of higher order polynomials (e.g. LEG(5)). Overall, higher order polynomials are needed for interpolation, and especially, for extrapolation of yields.
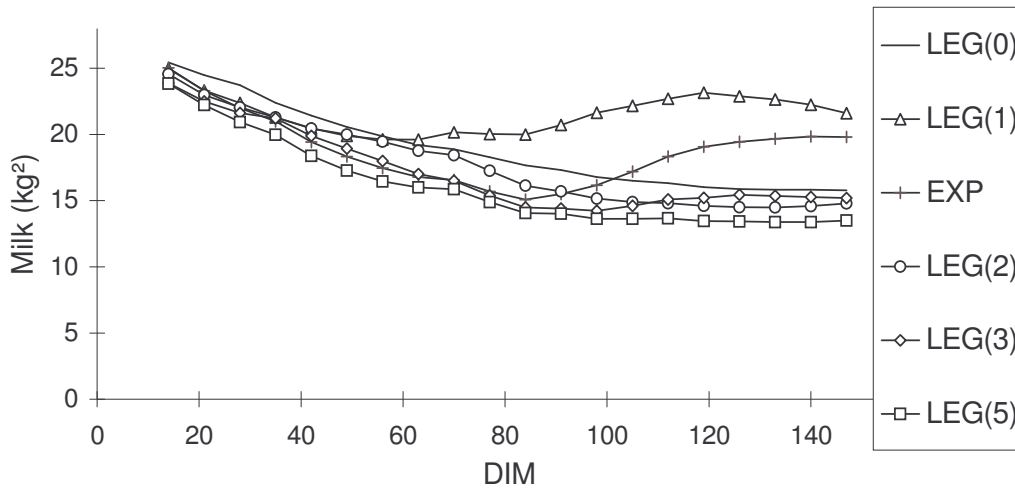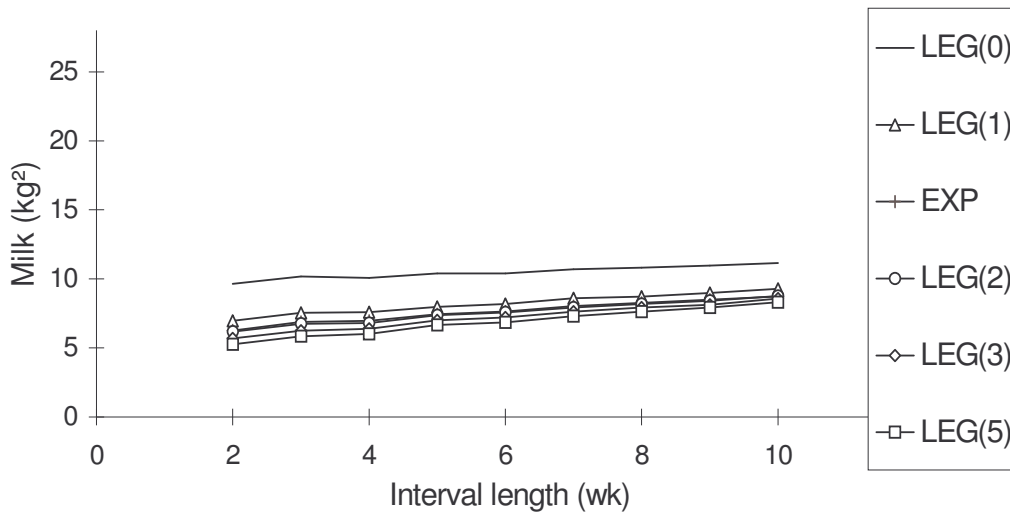

Figure 6. Mean square error of predictions of missing observations from a test-day model using Legendre polynomials of different orders of fit [LEG(m)] and an exponential function (EXP) for subsets with varied test-day intervals.

DISCUSSION

Phenotypic lactation curves have been fitted for individual lactations according the RRM approach in a data set where daily milk yields were recorded every week, i.e. the milk yield data was more complete than in commercial herds. The more frequent milk recordings implied that there was more information about the shape of the lactation curve.

The number of cows in this study was too small to estimate genetic and environmental lactation curves, which requires a much larger data set. It is expected that when the function used to model the environmental and genetic curve is the same, that it will be identical to the phenotypic curve. Analyses, where the genetic and the environmental lactation curve differ, seem prone to erroneous estimates of variance. For instance, when the environmental curve has fewer parameters than the genetic curve, the greater flexibility of the genetic curve may be used to fit changes in the environmental curve, which can lead to very high estimates of heritability (Kettunen et al, 1998). If the environmental and genetic curve are the same, both curves are equally, well equipped for fitting the environmental, respectively, the genetic (co)variances. In order to avoid problems of environmental variances being fit by the genetic

curve, and vice versa, it may be recommended to use the same curve for the environmental and genetic curves, which is equal to the phenotypic curve, that was investigated in this paper.

Different orders of fit of normalized orthogonal Legendre polynomials were used to model the individual deviations from the average lactation curve instead of conventional polynomials, i.e., a linear regression on [1, DIM, DIM^2, DIM^3, etc.]. When conventional polynomials were used the parameters σ_e^2, MSEP, and (co)variances of milk yields modeled between and among DIM (Figures 1, 2, and 4) were close to those obtained from the Legendre polynomials of the same order of fit (results not shown). The EM-REML algorithm used to estimate the covariate matrices converged faster when Legendre polynomials were used, and higher order Legendre polynomials did converge where conventional polynomials failed.

The criteria for the goodness of fit of different curves in the RRM approach were 1) a graphical comparison of the (co)variances for milk yields over and among DIM modeled by the different TDM versus the observed (co)variances; and 2) comparing test-day yields based on the observed value and the predicted one in a subset, i.e. when a test-day yield was missing (MSEP). The criterion MSEP is preferred over maximum likelihood, because it quantifies the ability of a model to inter- or extrapolate milk records, which is required in practice. The significance of a likelihood ratio test depends on the amount of data available, i.e., it tells us whether there is enough information in the data to fit a more sophisticated model, and not the ability to handle missing data as investigated by MSEP.

It was expected that first criterion would improve as the number of parameters in a TDM increased. Hence, the higher order Legendre polynomials were expected to yield the best fit with respect to this criterion, which was found when comparing the Figures 3 and 4. That the criterion MSEP improves as the number of parameters in the curve increases is not obvious. This is because the different models have to inter- and extrapolate to predict missing test-day yields. A curve with too many parameters may yield poor inter- and extrapolation results, because extra parameters make the curve bend towards or through the data points, but the resulting bends may be odd and lead to poor predictions at places where there are no data points. Especially in the case of extrapolation, an odd bend of the curve at the end of the known data points can yield very poor predictions outside the range of the data points.

However, in general, the MSEP criterion did improve as the order of fit of the Legendre polynomial increased. This was probably because the higher order components were estimated as random effects, which implies that they were regressed towards zero (especially if there was little information for their estimation). The general improvement of MSEP with the order of fit did not hold for LEG(0), which performed remarkably well, given its low order of fit. This was probably due to the robustness of the LEG(0) model. However, LEG(0), did not account for

persistency of the lactation curves, and its MSEP was worse than that of LEG(5). Hence, the criterion MSEP seemed to favor the model LEG(5) or an even higher order polynomial.

LEG(5) provided also a good fit, compared to LEG(0), when compared with the observed correlation structure obtained from the model FIXED. More smoothing and a lower number of parameters to estimate per animal favors LEG(5) over the higher order Legendre polynomials, LEG(6) and LEG(7).

Figures 1 and 2 showed that the variances over DIM modeled by the different TDM were not accurate, when compared with the observed values obtained from the model FIXED. This holds especially later in the lactation. The poor modeling of the variances later in lactation may be due to the smaller number of observations in that part of the lactation, due to missing records at the end of lactation. A heterogeneity of variances correction, where Var($\mathbf{y}$) is corrected towards the values that are expected by the model [e.g. Meuwissen et al., 1996], could solve the poor resemblance between variances observed and modeled in the Figures 1 and 2. Not accounting for the effect of pregnancy status at the day of test might have influenced the variance modeled, especially later in the lactation. The effects of incomplete lactation records, heterogeneity of variances correction, and pregnancy status will be investigated in another paper.

The variance components modeled by the different TDM were estimated directly from the data, whereas they can also be estimated from the observed covariate matrix between DIM (Kirkpatrick et al., 1994), which are shown in Figure 3. Although this is computationally less demanding, it does not yield maximum likelihood estimates of the variance components. When LEG(4) was fitted by estimating (co)variances components from the (co)variance matrix of DIM observed (obtained from the model FIXED), especially, the MSEP criterion was increased compared with when the original variance components (Table 1) were used (results not shown).

The phenotypic predictions of the random regression coefficients estimated with, e.g., LEG(5) could be used for a multi-trait breeding value evaluation as a two step procedure. The predicted error variances of the predicted random regression coefficients might than be used as weighting factors in the breeding value evaluation. Although computationally this approach will be less demanding, simultaneous estimation of random genetic and permanent environmental effects and fixed effects is probably preferred (as in Jamrozik et al., 1997b). Based on the present results, LEG(5) seems to be the preferred curve for a simultaneous fit of genetic and permanent environmental effects.

CONCLUSIONS

The model LEG(5) yielded overall the best fit of the individual phenotypic lactation curves of the models that were investigated, i.e. EXP and LEG(0-7). However, at the end of lactation, the variances of milk yields over DIM modeled by LEG(5) were not very accurate. This effect may probably disappear if more complete records are used, a correction for the pregnancy status at the day of test was applied and may be solved by a correction for heterogeneous variances. Since the phenotypic model LEG(5) yielded a good fit for phenotypic lactation curves, it is expected to yield also a good fit for environmental and genetic curves in a genetic TDM for breeding value evaluation.

————————

Reduction of the number of parameters needed for a polynomial random regression test-day model.

(M. H. Pool[a,b], and T.H.E. Meuwissen[b])

[a] Wageningen Institute of Animal Science (WIAS).

[b] Department of Genetics and Reproduction. Institute of Animal Health and Science (ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

ABSTRACT

Legendre polynomials were used to describe the (co)variance matrix within a random regression test-day model. The goodness of fit depended on the polynomial order of fit, i.e. number of parameters to be estimated per animal but is limited by computing capacity. Two aspects: incomplete lactation records and heterogeneous variances were investigated to reduce the order of fit needed. Analysis of the original data set, which contained 50% incomplete lactation records, required a fifth order of fit and showed too high variances at the end of the lactation.

Variance component estimates from only complete lactation records improved the goodness of fit. Correlations estimated were more alike those observed and substantially lower variances at the end of lactation were obtained, such that a fourth order seemed sufficient. Correction for heterogeneous variances across classes of days in milk improved the estimated correlation structure further and the mean square errors of prediction were better, resulting in a third order of fit being sufficient. Overall, use of only complete lactation records for parameter estimation and correction for heterogeneous variances allowed a reduction of two parameters that need to be estimated per animal.

INTRODUCTION

Genetic evaluation models in dairy cattle that use test-day records instead of (305-d) lactation records are of great interest in the area of cattle breeding for production traits (e.g. Schaeffer and Dekkers, 1994; Kettunen et al., 1998; Veerkamp and Goddard, 1998; Pool and Meuwissen, 1999). These models are also used for traits such as feed intake (Veerkamp and Thompson, 1998), live weight (Koenen and Veerkamp, 1998) and longevity (Veerkamp et al., 1999). The models for production traits are known as test-day models (**TDM**) and can account for the effect of test date (Reents and Dopp, 1996), number, order and intervals between test-day records, and provide information about persistency by modeling the pattern of the lactation curve (Schaeffer and Dekkers, 1994).

Different types of TDM are described in the literature (see review by Swalve, 1995). TDM describe longitudinal measurements which change over time, i.e. for milk production the model has to allow a continuous change of variances and covariances of test-day yields during the lactation period. In the random regression approach (Schaeffer and Dekkers, 1994) the lactation curve is split into two parts: a fixed part (average lactation curve) and a random animal specific part (deviations from the average curve). The variance components of the random regression coefficients determine the covariance function of each pair of days in milk (**DIM**).

In the literature, several lactation curves were investigated to describe the covariance function (e.g. Ali and Schaeffer, 1987; Kirkpatrick et al., 1994; Guo and Swalve, 1997a; Jamrozik et al., 1997a; Pool and Meuwissen, 1999). Generally, the goodness of fit increased with the number of function parameters describing the curve. Although differences between functions were small, Guo and Swalve (1997a) recommended exploiting those. Besides a more simple and understandable model, the number of parameters to be estimated per animal is limited for computational reasons.

Jamrozik and Schaeffer (1997) and Kettunen et al. (1998) showed unexpected high estimates of heritabilities for daily yields as well as negative genetic correlations between the most distant tests days when using the Ali and Schaeffer curve (1987) as the random regression function. Kettunen et al. (1998) concluded that the overestimation of the genetic variances at the edges of the defined lactation curve trajectory was likely due to the mathematical characteristics of the sub-model, i.e. the function chosen within the TDM. Another type of function, Legendre Polynomials (**LEG**, Kirkpatrick et al., 1990) was applied more recently in several TDM-studies (e.g. Kirkpatrick et al., 1994; Veerkamp and Goddard, 1998a; Pool and Meuwissen, 1999). Kirkpatrick et al (1994) choose LEG, as one out of the family of orthogonal functions, because they expected a relatively smooth covariance function based on polynomials underlying the growth curve. Although the choice of which type of function to use might not have a large effect on the parameter estimates within the interval that data was collected, the function might be more important as soon as data are extrapolated (Kirkpatrick et al., 1990). Meyer (1998) observed that data points at the beginning and end of the lactation trajectory for which an animal has records have a relatively large impact on the regression coefficient estimates, when polynomials are used as the covariance function.

Incomplete lactation records might affect the weighting of data points because the model has to extrapolate the lactation record. Further most models assume that the residuals are distributed normally and independent with zero mean and equal variance, but in practice a systematic pattern was observed in the residuals over the lactation trajectory (Jamrozik et al., 1997; Liu et al., 1998). The latter may be removed by heterogeneity of variance correction

over DIM. When one of these two aspects is significant, it may be expected that by including it in the model, a lower order of fit can be achieved without significantly reducing the goodness of fit of the model.

This study investigated the effect of two aspects, namely, incomplete lactation records and heterogeneous variance over DIM on the estimated covariance function parameters, especially at the outer parts of the trajectory. The aim of this study was to minimize the order of fit of Legendre polynomials within the TDM, i.e. to reduce the required number of parameters to be estimated per animal in order to make the application of the TDM feasible in practice.

MATERIAL AND METHODS
Data
The original data set contained 36,288 test-day records (weekly measured) from 951 lactations of 605 Holstein Friesian cows (536 first and 415 later parity) obtained from the experimental farm 't Gen (ID-Lelystad, The Netherlands). The lactations had variable length with a minimum of 150 days long and a maximum of 305 days (75% ≥ 230 days, 50% ≥ 293 days, and 25% ≥ 301 days). The average and standard deviation of test-day milk yield were 27.7 and 7.6 kg, respectively. For a more detailed description of the data see Pool and Meuwissen (1999).

For the effect of incomplete lactation records only full, completed lactation records, i.e. last test conducted at or after day 280 DIM and at least 22 tests were selected. Such lactation records describe the whole trajectory of 305 days, i.e. no longer any implicit extrapolation was embedded in the model. The selected data contained 15,907 test-day records from 370 completed lactation records, 192 first and 178 later parity, from 267 animals, with an average and standard deviation for test-day milk yield of 27.3 and 7.4 kg, respectively.

Both data sets, i.e. the original with 951 lactation records and the selected with 370 completed lactation records, were used. Covariance function parameters were estimated using the selected data set. Criteria for the goodness of fit of the models were calculated using the original data set with variance component estimates from the selected data.

Test-day Model
TDM with different orders of fit, based on Legendre polynomial (Kirkpatrick et al., 1990;1994), were applied to the data sets to determine the goodness of fit, i.e. the order of fit needed to model individual lactation curves accurately for the aspects investigated. The following TDM, as suggested by Pool and Meuwissen (1999) was used:

$$\text{LEG(m)}: \qquad y_{ij} = \mathbf{x_{ij}}'\boldsymbol{\beta} + \boldsymbol{\phi}_{ij(m)}'k_{i(m)} + e_{ij} \qquad [1]$$

where y_{ij} = test-day milk yield j in the animal × lactation i (i.e. lactations of the same animal were assumed independent); x_{ij}' = incidence row vector for fixed effects β; β = [μ; ys; age; cDIM; TD]' with respectively the overall mean, year season of calving, age at calving, weekly classes for DIM within first and later parity and test date effect (for details see Pool and Meuwissen, 1999); $\phi_{ij(m)}$' = $t_{ij} \Lambda_m$ where t_{ij} = (1 by m) row vector with standardized DIM (sDIM, ranging from –1 to 1) to the power 0,1,…,m, with m as the order fit and Λ_m = matrix of Legendre polynomial coefficients (Kirkpatrick et al., 1990); $k_{i(m)}$ = (m by 1) vector of random regression coefficients for animal × lactation i and e_{ij} = residual.

Models used to investigate the effect of incomplete lactation records and heterogeneous variance over cDIM were termed C-LEG(m) and H-LEG(m), respectively, were m specifies the order of fit of the Legendre polynomials applied. The random regression coefficients used for C-LEG(m) and H-LEG(m) were estimated from the selected data set, i.e. the 370 completed lactation records. All results were compared to previous results which were based on parameters estimates from all 951 lactation records, i.e. the reference model, termed as model LEG(m), as described in Pool and Meuwissen (1999).

Covariance function

The estimated covariance function of test-day records over DIM is:

$$\mathrm{Cov}(y_{ij}, y_{ij'}) = \phi_{ij(m)}' \mathbf{K}\, \phi_{ij'(m)} + \sigma_e^2 \qquad [2]$$

for j≠j', and where $\mathbf{K}$ = Var(k) = estimated variance-covariance matrix of the random regression coefficients over animal × lactations and of size m × m; σ_e^2 = residual variance. Furthermore the model assumed E($k_{i(m)}$) = 0, E(e_{ij}) = 0 and E(y_{ij}) = $x_{ij}\, \beta$. The covariance matrix of $k_{i(m)}$, i.e. $\mathbf{K}$, and σ_e^2 were obtained by Residual Maximum Likelihood estimation (REML, see Patterson and Thompson, 1971) and the expectation maximization algorithm (Henderson, 1984).

Correction for heterogeneous variances

A phenotypic correction for heterogeneous variances was applied over weekly classes of days in milk (2×44 classes within first and later parity) according to the method of Meuwissen et al. (1996). Estimation of variance components and calculation of scaling factors to correct for phenotypic heterogeneous variances over cDIM were carried out iteratively. The data vectors (y_i) were scaled (equation [4]), until the residual variances for each cDIM class i (equation [3]) were homogeneous and the REML estimates of the random regression

coefficients were converged, accounting simultaneously for all fixed and random animal $\times$ lactation effects. The residual variance and scaled observations were calculated as follow:

$$\hat{\sigma}^2_{e_{i(q)}} = \frac{\mathbf{y_{i(q)}}' \; \hat{\mathbf{e}}_{i(q)}}{n_i \; sc} \qquad [3] \qquad \mathbf{y_{i(q+1)}} = \mathbf{y_{i(q)}} \sqrt{\frac{\hat{\sigma}^2_{e_{o(q)}}}{\hat{\sigma}^2_{e_{i(q)}}}} \qquad\qquad [4]$$

where $\hat{\sigma}^2_{e_{i(q)}}$ = estimated residual variance for cDIM class i and $\hat{\sigma}^2_{e_{o(q)}}$ = overall residual variance in the model estimated in iteration q ($\hat{\sigma}^2_{e_{o(q)}}$ was re-estimated in each iteration, as the mean of $\hat{\sigma}^2_{e_{i(q)}}$); $\mathbf{y_{i(q)}}$ and $\mathbf{y_{i(q+1)}}$ = vector with the current and updated observations in the cDIM class i in iteration q, respectively; $\hat{\mathbf{e}}_{i(q)}$ = vector with residuals for cDIM class i in iteration q; n_i = number of observation in cDIM class i; sc = (N-rank($\mathbf{X}$))/N = scaling factor accounting for the degrees of freedom used by the model, where N = the total number of test-day records and $\mathbf{X}$ = design matrix of the fixed effects (one sc-factor was used for all cDIM classes, because sc_i = (n_i-rank($\mathbf{X_i}$))/n_i for cDIM class i could not be calculated since the design matrix $\mathbf{X_i}$ extends across cDIM).

Comparison of Models

The criteria for the goodness of fit used were as in Pool and Meuwissen (1999), namely : 1) A graphical comparison of the variance of the data (Var($\mathbf{y}$)), and 2) Mean square errors of predictions of missing observations (**MSEP**) for the different TDM.

The first criterion compares the pattern of the Var($\mathbf{y}$) predicted by the model and that observed between the residuals when only the fixed effects of the model were fitted. Hence, observed variances were obtained without imposing a structure on Var($\mathbf{y}$) and were termed as OBS and C-OBS for the original and reduced data set, respectively, for which correlation structures were calculated based on weekly classes of DIM. For all other models, Var($\mathbf{y}$) was estimated by equation [2], where $\mathbf{y}$ includes a record for each day in the lactation trajectory (1-305) and required estimates for Var($\mathbf{k}$) and σ^2_e. For model C-LEG(m) and H-LEG(m) those parameters were estimated using the selected data set and for model LEG(m) using the original data. The residual variance over DIM was assumed constant, for model C-LEG(m) and varied over cDIM for model H-LEG(m). The model with the best order of fit, is the model that expects a (co)variance and a correlation structure which is equal, i.e. same shape as the observed ones (OBS and C-OBS).

The second criterion, MSEP, investigates how well missing records could be predicted. Therefore, different patterns of records were deleted from the original data set to obtain subsets with missing records, i.e. part lactation records of different lengths were created. The deleted observations were predicted using the information in the subset and compared to the actually observed records [see Pool and Meuwissen (1999)]. MSEP were calculated as:

Table 2. Correlations between random regression coefficients using a third and fifth order fit Legendre polynomial expected by the model LEG(m), C-LEG(m) and H-LEG(m) (i.e. for the reference model, based on complete lactation records, respectively, after a correction for heterogeneity of variances of milk yield over days in milk classes within parity).

Model		$k0(m)$ [1]	$k1(m)$	$k2(m)$
LEG(m)	k1(3)	0.2879		
	k2(3)	-0.1705	0.0119	
	k3(3)	0.1756	-0.1040	-0.0740
C-LEG(m)	k1(3)	0.1106		
	k2(3)	-0.2851	-0.0282	
	k3(3)	0.1504	-0.1537	-0.3757
H-LEG(m)	k1(3)	0.3779		
	k2(3)	-0.1193	0.2248	
	k3(3)	0.2916	0.0490	-0.0657

	$k0(m)$	$k1(m)$	$k2(m)$	$k3(m)$	$k4(m)$
k1(5)	0.2291				
k2(5)	-0.2952	-0.0279			
k3(5)	0.1246	-0.1185	-0.1524		
k4(5)	-0.3441	-0.0356	-0.0757	-0.2653	
k5(5)	0.1838	-0.1835	-0.0472	-0.1663	-0.4297
k1(5)	0.1227				
k2(5)	-0.2893	-0.0178			
k3(5)	0.1903	-0.1116	-0.3326		
k4(5)	-0.3188	-0.0387	-0.0348	-0.2942	
k5(5)	0.1821	-0.1569	-0.0231	-0.1451	-0.5366
k1(5)	0.3567				
k2(5)	-0.0567	0.2205			
k3(5)	0.2948	0.0758	-0.0436		
k4(5)	-0.1629	-0.0482	-0.0316	-0.0451	
k5(5)	0.1052	-0.0487	0.0570	-0.0668	-0.1875

[1] $k_{j(m)}$ = random regression coefficient j in model LEG(m) using Legendre polynomials with an order of fit m.

$$\text{MSEP}_i = \sum_{j=1}^{s_i} (y_{ij} - \hat{y}_{ij})^2 / s_i \qquad [5]$$

where y_{ij} = missing record j in subset i, which was known in the complete data set; $\hat{y}_{ij}$ = predicted value of missing record j in subset i, and s_i = number of the missing records in subset i. The pattern in MSEP was expected to decrease steadily over DIM if information accumulates, i.e. if part lactations become longer. The model with the lowest and continuously decreasing MSEP-pattern has the best fit.

RESULTS

Variance Estimates

      Residual variances for milk yield estimated for the models LEG(m), C-LEG(m) and H-LEG(m) are given in Table 1. Estimates decreased with the order of fit for all models but differences were small for the higher orders of fit. Between models, estimates can not be compared because estimates

Table 1: Residual variances of daily milk yield (kg²) estimated by the model using Legendre polynomials with an order of fit m for LEG(m) [the reference model, based on the original data] and the models C- and H-LEG(m) (based on complete lactation records, respectively after a correction for heterogeneous variances over days in milk classes within parity).

Model	LEG(m)	C-LEG(m)	H-LEG(m)	Model	LEG(m)	C-LEG(m)	H-LEG(m)
LEG(0)	9.39	9.15	9.07	LEG(4)	4.61	4.50	4.43
LEG(1)	6.56	6.56	6.49	LEG(5)	4.38	4.23	4.17
LEG(2)	5.53	5.47	5.43	LEG(6)	4.20	4.09	4.05
LEG(3)	4.96	4.85	4.84	LEG(7)	4.07	3.99	3.93

      for H-LEG(m) were on a different scale as for C-LEG(m) and LEG(m). Variances and covariances were estimated and presented in the form of correlations between the random regression coefficients k_i and k_j for the order of fit m ($r_{k_{i(m)}, k_{j(m)}}$ and $i \neq j$) in Table 2 and are comparable between the models. Values showed differences between the models LEG(m), C-LEG(m) and H-LEG(m) and varied also slightly with the order of fit (estimated up to a seventh order of fit). Correlations ranged for LEG(m) from -0.51 to 0.52 ($r_{k0(0),k1(0)}$ and $r_{k5(6),k6(6)}$,

Figure 1: Variances of milk yield observed by a test-day model based on complete lactation records (model C-OBS) and expected for the order of fit 0, 1 and 3 using Legendre polynomials [C-LEG(m), based on the selected data], compared with the variances observed versus expected by the reference model [OBS and LEG(m), based on the original data, chart in upper right corner].
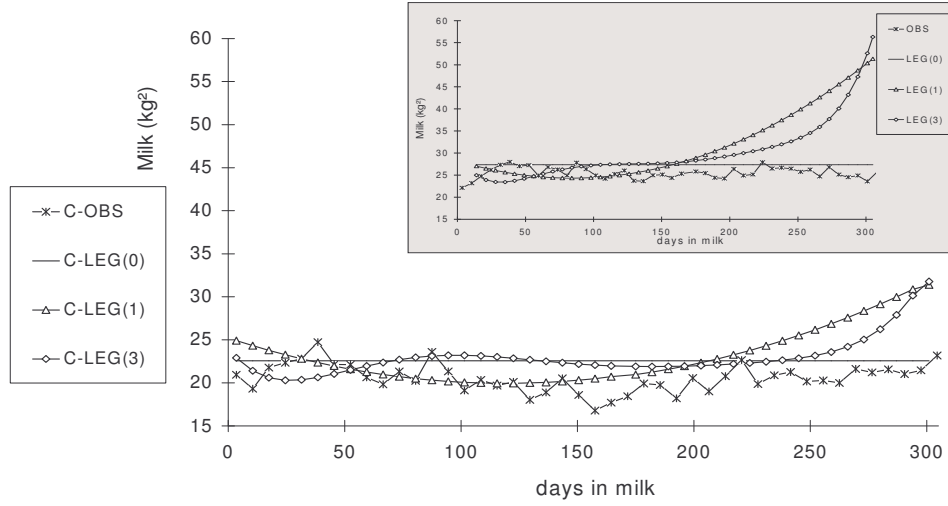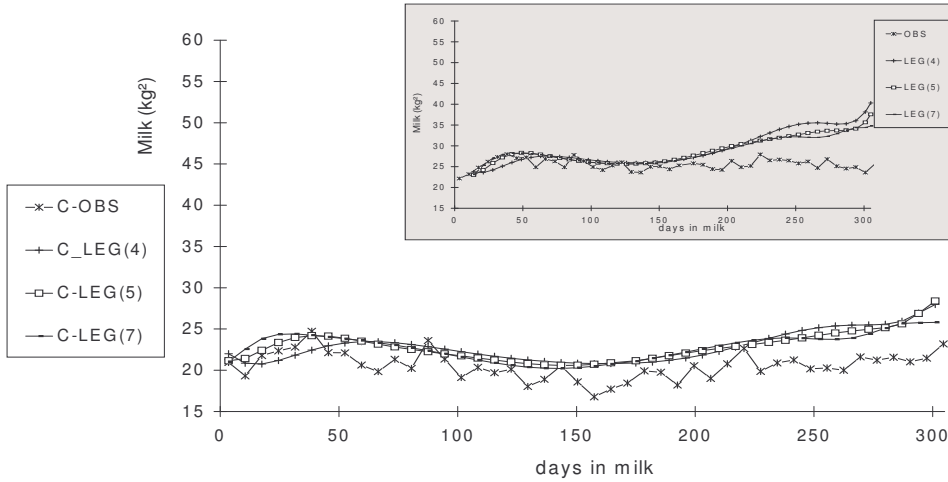

Figure 2: Variances of milk yield observed by a test-day model based on complete lactation records (model C-OBS) and expected for the order of fit 4, 5 and 7 using Legendre polynomials [C-LEG(m), based on the selected data], compared with the variances observed versus expected by the reference model [OBS and LEG(m), based on the original data, chart in upper right corner].

respectively), for C-LEG(m) from -0.64 to 0.23 ($r_{k1(7),6(7)}$ and $r_{k5(6),6(6)}$ respectively) and for H-LEG(m) from –0.33 to 0.39 ($r_{k5(7),6(7)}$ and $r_{k0(2),k1(2)}$, respectively) (only results for the third and fifth order of fit are presented in Table 2). Although correlations were in general not very strong, they were not negligible. Where C-LEG(m) estimated the strongest (negative) correlation between the higher order random regression coefficients, H-LEG(m) estimated the strongest (positive) correlation between the lower order random regression coefficients.

Modeled versus Observed Covariances

The covariances of milk yields expected by each model [LEG(m), C-LEG(m) and H-LEG(m)] were calculated from the (co)variance matrix of random regression coefficients (kj(m)) and the residual variance for each DIM (equation [2]). In Figures 1 and 2 the variances observed in the data and expected are presented for the reference model [LEG(m), charts in the upper right corner, described by Pool and Meuwissen (1999)] and C-LEG(m) (main graphs). The shape of the variance curve expected for the different orders of fit should be compared to the observed ones, i.e. OBS in the upper graphs and C-OBS in the main graphs. In general, the goodness of fit increased with the order of fit for both models. However, the variances expected by C-LEG(m) (i.e. using only complete lactation records of at least 280 days long) approximated the observed variances better than model LEG(m) did. Figure 3 shows the expected variances of the records that were corrected for heterogeneous variances. [H-LEG(m)]. The patterns of the curves in Figure 3 are different from those of the other
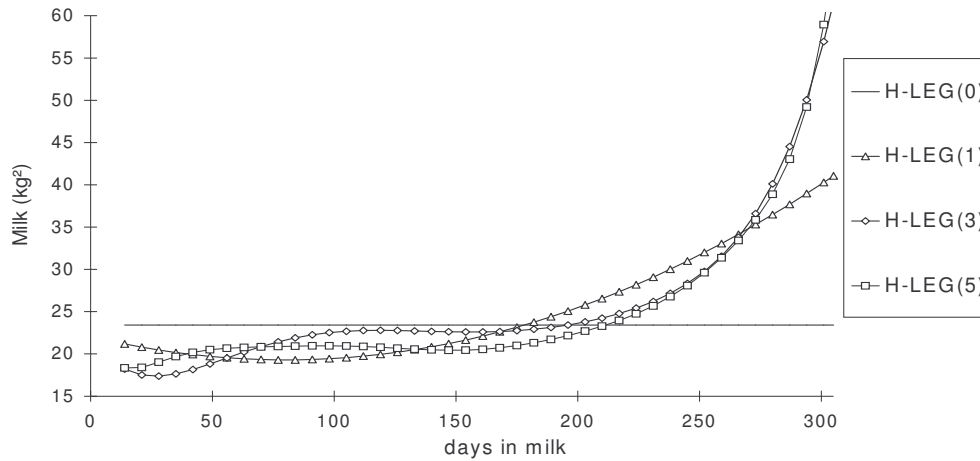
Figure 3: Variances of milk yield expected by a test-day model using Legendre polynomials after correction for heterogeneity of variance for milk yield over cDIM classes for an order of fit of 0, 1, 3 and 5 [i.e. H-LEG(m), based on complete lactation records].

37
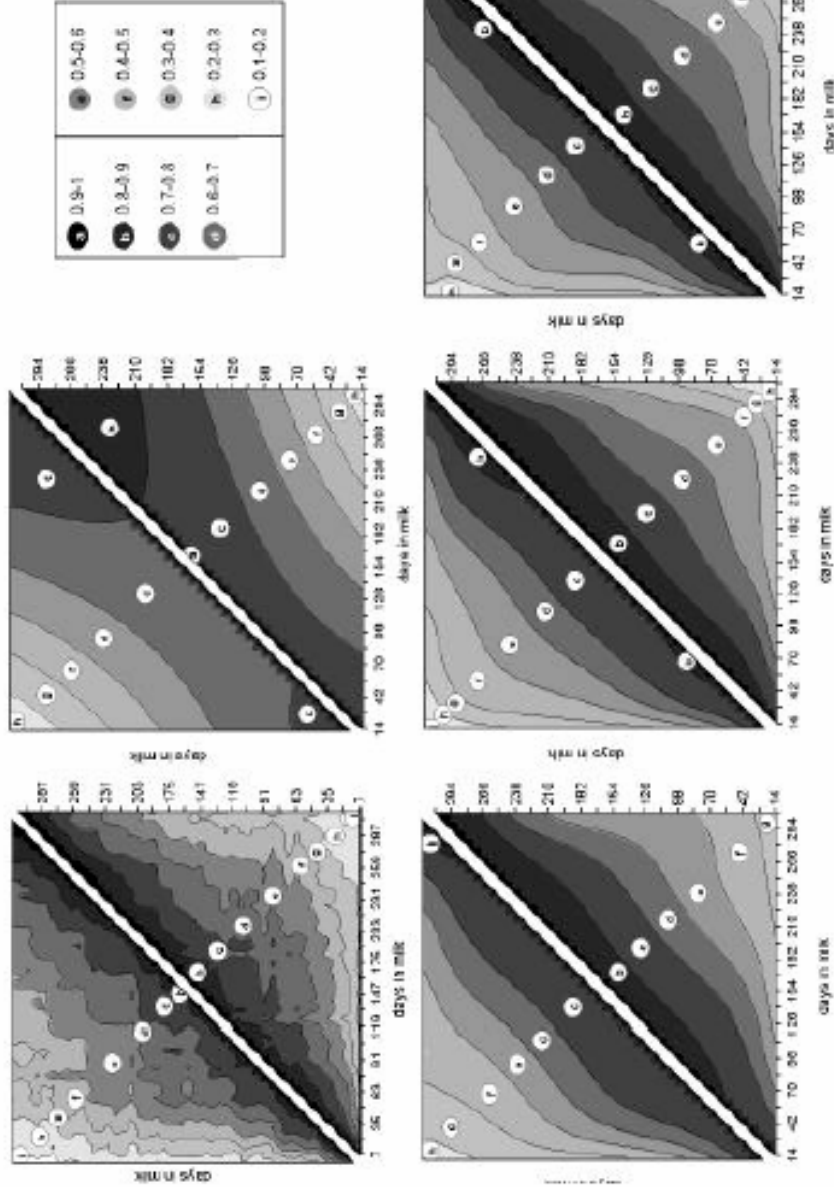
Figure 4: Correlation structures for milk yield among days in milk observed in the data (OBS and C-OBS) and those expected by a test-day model using Legendre polynomials with different orders of fit m based on the selected data with lactation records of at least 280 days long [C-LEG(m)], compared to those for the reference model [LEG(m)], based on the original data set. Stacked areas on top, from left to right, are OBS (lower triangle) and C-OBS (upper triangle); LEG(1) (lower triangle) and C-LEG(1) (upper triangle). Stacked areas on bottom, from left to right, are LEG(3) (lower triangle) and C-LEG(3) (upper triangle); LEG(4) (lower triangle) and C-LEG(4) (upper triangle); LEG(5) (lower triangle) and C-LEG(5) (upper triangle).

models [LEG(m) and C-LEG(m)] and not comparable because the variances of the corrected records were scaled towards the variances expected by the TDM. Variance estimates for all H-LEG(m), except H-LEG(0), which was constant, increased towards the end of the lactation trajectory, starting halfway the lactation period, with the most rapid increase for the higher orders of fit.

Based on complete lactation records the variance pattern expected was sufficiently accurate for model C-LEG(4) , where the reference model needed LEG(5). The increase at the end of the lactation period for the reference model [LEG(4)] was not observed for C-LEG(4) for which random regression coefficient estimates from the reduced data set were used. For H-LEG(m) the data was scaled such that the observed variance equals the variance that was expected by the model, which means that the choice of the model did no longer depend on the expected covariance matrix, but on the correlation matrix.

Expected versus Observed Correlation Structures

The expected and observed correlation structures for C-LEG(m) and the reference model, LEG(m), are presented in Figure 4. The correlation structure observed in the data changed slightly towards the end of the lactation period, showing a tendency for somewhat lower correlations between days early in lactation and higher between days late in lactation for the reduced data set compared to the original data set [C-OBS and OBS, respectively]. The observed correlation structure shows the overall pattern clearly, although the observed correlations were not smoothed. Observed correlations were calculated for weekly classes of DIM so that number of observations was large enough for each class given the size of the data set. Reducing the class length for DIM and a larger data set is expected to smooth the observed correlations more.

In general the correlation structure was modeled better for the higher orders of fit for both models, C-LEG(m) and LEG(m). Estimated correlations ranged from almost unity for successive days to almost zero for days far apart. The correlation structures expected with model C-LEG(m) seemed to fit the observed one better as those from model LEG(m). For model C-LEG(m) a fourth order of fit Legendre polynomial seemed to fit the observed structure in the data accurately. The fit of C-LEG(4) was better than C-LEG(3) because stacked areas showed a slightly odd bend between days in the middle of the lactation, especially for the lower correlation areas, which was generated probably by the increased variances expected at the end of the lactation (see Figure 1). Compared to C-LEG(5) the goodness of fit of C-LEG(4) was more smoothed, suggesting that C-LEG(4) would be less sensitive to uncertainties in the data. Based on the expected covariance and correlation pattern (Figure 2 and 4) C-LEG(4) and C-LEG(5) were almost identical suggesting that the order of fit, i.e. the number of parameters to be estimated per animal could be reduced by one to a fourth order of fit.

The correlation structures expected by the model after correction for heterogeneity of variances [H-LEG(m)] were presented in Figure 5. The scaling of the covariance matrix in the data towards the expected one resulted in a better fit of the observed correlation structure (C-OBS in figure 4) compared to model C-LEG(m), especially for days late in the lactation [e.g. the observed stacked correlation range 0.8-0.9 after day 210 observed in the data was expected by H-LEG(3), but not by model C-LEG(3)]. Overall, H-LEG(3), two orders of fit lower than the reference model [LEG(5)], seemed to yield a good fit of the correlation structure observed in the reduced data.
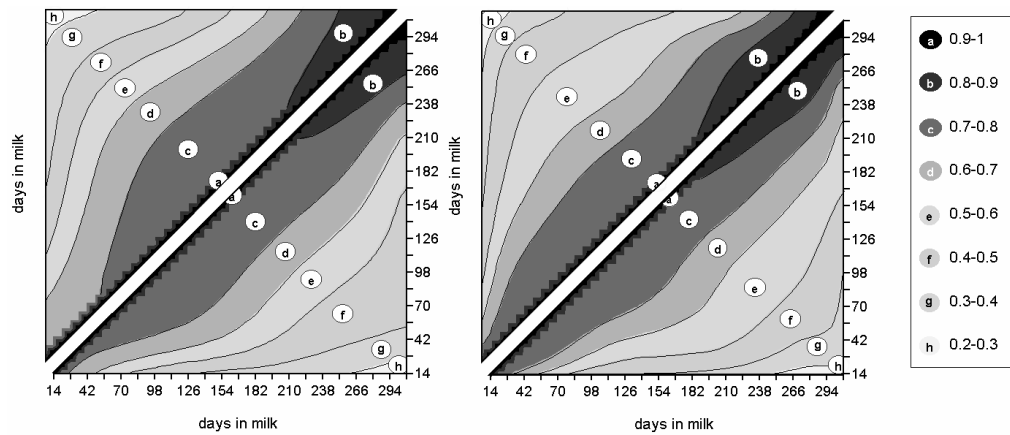
Figure 5: Correlation structures for milk yield among days in milk expected by a test-day model using Legendre polynomials with different orders of fit m after correction for heterogeneity of variances of milk yields over classes for days in milk [H-LEG(m)]. Stacked areas, from left to right, are H-LEG(2) (upper triangle) and H-LEG(3) (lower triangle); H-LEG(4) (upper triangle) and H-LEG(5) (lower triangle).

MSEP of Missing Observations

In Figure 6 (left chart) the MSEP is given for several subsets with part lactations of different lengths for the reference model [LEG(m)] and for the model C-LEG(m). The MSEP was expected to decrease continuously if information accumulates, i.e. if part lactation become longer. For the lower orders of fit up to a third order the MSEP decreased with lactation length for part lactations up to a length of 80 DIM but increased thereafter. Overall, model C-LEG(m) was more consistent when information accumulated compared to the reference model [LEG(m)]. Comparing different orders of fit for C-LEG(m) the MSEP-pattern improved up to C-LEG(4) and was stable for higher orders of fit (Figure 6, right chart).

A correction for heterogeneity of variance improved the MSEP-pattern further, especially for the lower orders of fit, up to LEG(3) (Figure 7, left chart). The MSEP for H-LEG(m)

Figure 6: Mean square error of predictions of missing observations from a test-day model using Legendre polynomials of different orders of fit m for the reference model [i.e. LEG(m)] and C-LEG(m) [i.e. based on complete lactation records with last test day at or after day 280], for several subsets with different part lactation lengths.

improved especially when part lactation records of 80 days and longer had to be extrapolated implicitly by the TDM. The unexpected increase of MSEP, when part lactation records of 100 days or longer were used, was almost stabilized completely for the lower orders of fit in model H-LEG(3) compared to C-LEG(m) (Figure 7, left chart). For the higher order of fits [H-LEG(2) and higher] MSEP-patterns were stable (Figure 7, right chart).
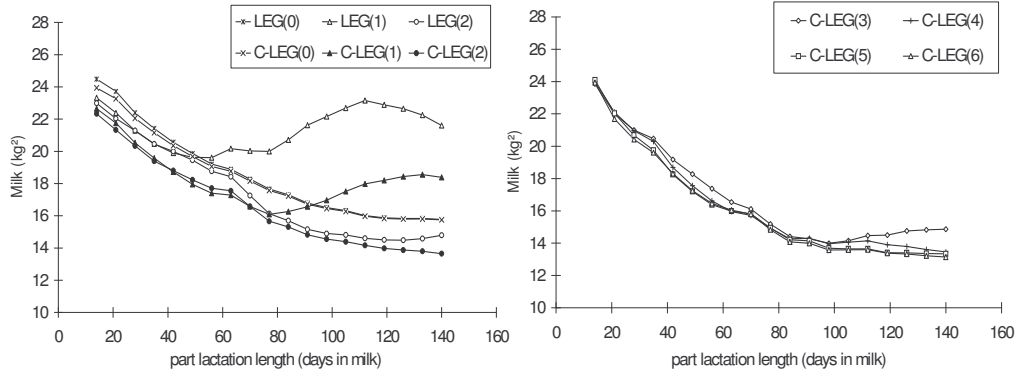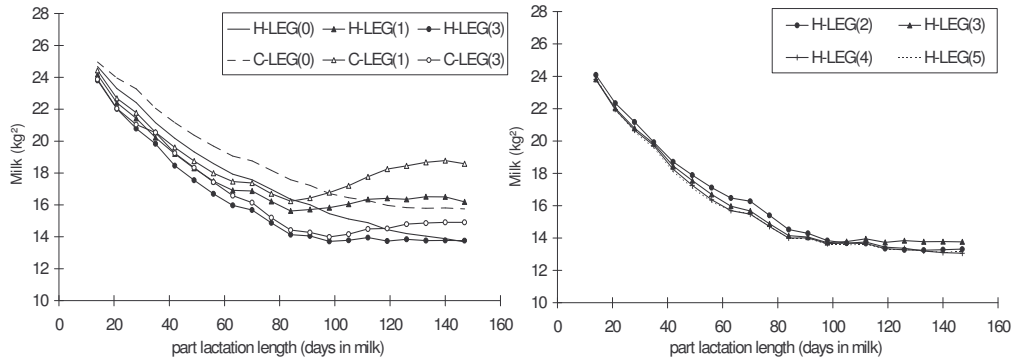

Figure 7: Mean square error of predictions of missing observations from a test-day model using Legendre polynomials of different orders of fit m for the model H-LEG(m) with correction for heterogeneity of variance of milk yields over classes for days in milk and based on only complete lactation records [i.e. C-LEG(m)] for several subsets with different part lactation lengths.

Overall, the results for MSEP showed that including information about test-day records at the end of the lactation period was important in order to get accurately estimated model parameters, i.e. lactation records with information over the whole lactation period should be used. Further, the unexpected increase of MSEP probably generated due to unequal weighting of the data points was improved clearly after the correction for heterogeneity of variance.

DISCUSSION

The aim of this study was to determine the minimum order of fit (i.e. reducing the number of parameters to be estimated per animal) without significantly reducing the goodness of fit for the expected variance-covariance matrix using Legendre polynomials in a random regression TDM. The goodness of fit was measured here by MSEP and a graphical comparison of the observed versus expected variance and correlation structures. Differences in goodness of fit could be compared by maximum likelihood tests, but for breeding value estimation the accuracy and fluctuations of predictions as information accumulates are more important (Pool and Meuwissen, 1999). The model suggested here will be developed further into a multi-trait, multi-lactation random regression TDM for genetic evaluations, which should have as few parameters as possible because of limited computer resources and to avoid estimation errors of redundant parameters.

The current data set was too small to estimate separated genetic and environmental lactation curves. It was expected that if the same function was used to model the environmental and genetic curve as suggested by Kettunen et al. (1998), that it will be identical to the phenotypic curve (Pool and Meuwissen, 1999). Hence, the presented results for the phenotypic parameter estimates are expected to hold also for genetic and environmental parameter estimate, although this is not known for certain. First and later lactations were modeled by the same covariance function. Having separate covariance functions for first and later lactation might be preferred but requires a larger data set. Further, the same data set was used for the estimation of parameters and for the verification in the calculation of MSEP, because there was no data set available with test-day records measured more frequently as on commercial farms.

Two aspects, incomplete lactation records and heterogeneous variances were investigated with respect to the goodness of fit of the TDM and the order of fit needed. Use of incomplete lactation records was expected to affect the estimation of model parameters unfavorably, since extrapolation can affect the weighting of data points unequally (Kirkpatrick et al., 1990) with relatively more weight at the ends of the recorded trajectory (Meyer, 1998). To avoid implicitly generated extrapolation within the model only complete lactation records were used. Estimation of random regression parameters and therefore the goodness of fit of the model improved in general and the order of fit required to model the observed variance and

correlation structure accurately was sufficient with a fourth order polynomial [C-LEG(4)], i.e. one order of fit less as in the reference model.

Discarding the incomplete lactation records may have introduced a selection bias in the data, e.g. maybe poor producing cows did not get the chance to complete the lactation. However, this possible selection bias seemed to have little effect on the observed variances for daily milk yields (see OBS and C-OBS in Figure 1) and the MSEP improved when variance component estimates from the reduced data set were used instead of from the original data set (Figure 6). A complete multi-trait approach, with each DIM as a different trait, could account for this selection bias, but is computationally not feasible. Although bi-variate analyses could be used as an approximation to the full multi-trait approach, the same selection bias would occur, because bi-variate analyses of traits at the end of the lactation requires selection of cows that have complete lactation records. The results presented for the TDM suggested that the selection bias due to selecting only complete lactation records was less severe than the bias that was introduced by the poor extrapolation of the polynomial random regression function when all lactation records were used. In conclusion, estimation of polynomial random regression coefficients was more biased by use of incomplete lactation records and therefore only complete lactation records should be used.

Correction for heterogeneity of variance for milk yields over cDIM within first and later parity was expected to correct for the systematic pattern observed in the residual terms over DIM (Jamrozik et al., 1997a; Liu et al., 1998; Pool and Meuwissen, 1999). A phenotypic correction before hand by scaling the data or afterward by correcting for the residual terms in the genetic evaluation (Kistemaker and Schaeffer, 1998) is possible. Here we opted for joint estimation of breeding values and heterogeneous variances (Meuwissen et al., 1996) because by this method the observed variances are scaled towards the variances expected by the model. Hence, the random regression part of the TDM, modeled not the (co)variances but only the correlations between the test-days. The latter improved the goodness of fit (Figures 5 and 7) such that H-LEG(3) seemed to yield a similar fit as C-LEG(4), i.e. a further reduction of one order of fit was achieved. Compared to H-LEG(4) the correlation structure estimated by model H-LEG(3) was more smoothed which suggested that it will damp out the sampling errors for the estimated random regression coefficients better. Compared to C-LEG(3), H-LEG(3) yielded better MSEP for part lactations with a length of 100 days or more (Figure 7), correlation structure predicted was as good as C-LEG(3) (figure 4 and 5) and the over-estimation of variance after day 250 (Figure 1) was corrected for in model H-LEG(3).

In the algorithm for heterogeneity of variance correction the random regression coefficients and scaling factors were estimated iteratively in two steps. Step 1: estimate heterogeneity of variance correction factors (Equation [3]); Step 2: perform iteration on variance components by the Expectation Maximization REML algorithm (Patterson and

Thompson, 1971; Henderson, 1984). These two steps were repeated until all estimates converged. This iteration was found to be faster than iteration on each step separately until convergence. Total number of iterations for the estimation of model parameters H-LEG(m) was three times as much as for the model C-LEG(m), for all orders of fit. For correction of heterogeneity of variance alone the number of iterations was somewhat less than for model parameter estimation. However, computer time for one round of correction took longer than one round of variance component estimation, thus time in total was approximately six times as much as for C-LEG(m).

Heterogeneous variance along the lactation trajectory was corrected for by the method of Meuwissen et al. (1996). With this method the variance of the data was scaled towards the expected variances by the model. Both the fixed and random effects were scaled toward the values expected by the model. The method was justified if it is used to scale heterogeneity of variance in the data, but questionable if it is used to scale, for example, a variance peak expected by the model but not observed in the data. In the latter case, the scaling of fixed effects is not justified, because observations in the same fixed effect class can be scaled differently. An alternative, would be to exclude the fixed effect from the scaling (formula [4]), i.e. to pre-correct test-day yields for fixed effects before the heterogeneity standardization and add them back afterwards. Changing the fixed effect correction of cDIM would not affect the results because cDIM levels are within subclasses of correction of heterogeneous variances. Further research is needed to test whether heterogeneity of variance correction without scaling of fixed effects would improve the goodness of fit of the RRM further.

CONCLUSIONS

The order of fit needed to model the expected pattern of the variance-covariance matrix accurately could be reduced with one order of fit, to a fourth order Legendre polynomial, by using only complete lactation records for the estimation of variance components. Alternatively, at the same order of fit, the variance components that were estimated in the data set with complete lactation records resembled the observed variances and correlations better, especially at the end of lactation. After applying a correction for heterogeneous variances the order of fit needed could be reduced further to a third order polynomial. Overall a reduction of two regression coefficients to be estimated per animal fewer was achieved without reducing the goodness of fit of a random regression test-day model using Legendre polynomials.

ACKNOWLEDGEMENTS

44

————————

Genetic parameters of Legendre polynomials for first parity lactation curves.

(M. H. Pool[a], L.L.G. Janss[b], and T.H.E. Meuwissen[b])

[a]   Wageningen Institute of Animal Science (WIAS).
[b]   Department of Genetics and Reproduction. Institute of Animal Health and Science
(ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

ABSTRACT

Variance components of the covariance function coefficients in a random regression test-day model were estimated by Legendre polynomials up to a fifth order for first parity records of Dutch dairy cows using Gibbs sampling. Two Legendre polynomials of equal order were used to model the random part of the lactation curve, one for the genetic component and one for permanent environment. Test-day records from cows registered between 1990 to 1996 and collected by regular milk recording were available. For the data set, 23,700 complete lactations were selected from 475 herds sired by 262 sires.

Because application of a random regression model is limited by computing capacity, we investigated the minimum order needed to fit the variance structure in the data sufficiently. Predictions of genetic and permanent environmental variance structures were compared with bivariate estimates on 30-d intervals. A third order or higher polynomial modeled the shape of variance curves over DIM with sufficient accuracy for the genetic and permanent environment part. Also the genetic correlation structure was fitted with sufficient accuracy by a third order polynomial, but, for the permanent environmental component, a fourth order was needed. Because equal orders are suggested in the literature, a fourth-order Legendre polynomial is recommended in this study. However, a rank of three for the genetic covariance matrix and of four for permanent environment allows a simpler covariance function with a reduced number of parameters based on the eigenvalues and eigenvectors.

INTRODUCTION

Test-day models (**TDM**) recently have received much attention as a genetic evaluation model in dairy cattle. By using single test-day records instead of 305-d lactation records, a TDM can account for the effect of test date, number of records, interval between records, and order of test-day records (Reents and Dopp, 1996). Above that, there is no longer any need to project incomplete lactations beforehand (Swalve, 1995). Moreover, models using longitudinal measurements will include information about the pattern of a lactation curve for a cow (Schaeffer and Dekkers, 1994). Several types of TDM were described [for a review see

(Swalve, 1995)]: a repeatability model (Ptak and Schaeffer, 1993), a random regression model (**RRM**) (Schaeffer and Dekkers, 1994), a covariance function model (Kirkpatrick et al., 1994), and a multiple-trait approach with reduced rank (Wiggans and Goddard, 1996). In the repeat-ability model, each test-day record is assumed to be a measure of the same trait, in contrast to the multiple-trait model in which each test-day is modeled as a different trait. However, in the RRM and covariance function approach, a fixed average lactation curve and a random regres-sion for the individual deviations is used to model the lactation curve of a cow. Therefore, the RRM enabled us to model the shape of the lactation with a restricted number of parameters.

The first function applied to model the random part of the lactation curve in a RRM (Kettunen et al., 1998; Schaeffer and Dekkers, 1994) was the Ali and Schaeffer curve (Ali and Schaeffer, 1987); the Wilmink function (Wilmink, 1987a) also has been used (Jamrozik et al., 1996). More recently, Legendre polynomials (**LEG**) have been applied by Kirkpatick et al. (1994). Legendre polynomials, as used in this study, have the benefit that 1) the functions are orthogonal, which is useful for analyzing patterns of genetic variation (Kirkpatrick et al., 1990), 2) missing records can be predicted more accurately than with the Wilmink curve (Pool and Meuwissen, 1999), and 3) higher orders were estimable where conventional polynomials failed (Pool and Meuwissen, 1999) because of better convergence.

Although the number of parameters to be estimated per animal in an RRM is substantially lower than in the multiple-trait approach, the number of function parameters still restricts the feasibility of a TDM because of limited computing resources. Note that in a genetic RRM the same number of parameters fitted for the genetic part is needed for the permanent environmental part.

Initially, the animal component in the genetic RRM was modeled by a function for the genetic part but only by one parameter for the permanent environmental part (i.e., a zero-order polynomial) (Jamrozik and Schaeffer, 1997; Kettunen et al., 1998). As a result, predictions of genetic variances were overestimated at the extremes of the lactation curve. The correlations between DIM became negative for days further apart, and heritabilities were highest at the beginning and end of lactation (Jamrozik et al., 1997a; Kettunen et al., 1998), which was unexpected and in contrast to those observed from multivariate analysis (Meyer et al., 1989; Pool and Meuwissen, 1999; Pander et al., 1992; Wiggans and Goddard, 1996). When the genetic and permanent environmental components were modeled both by a polynomial regression, predictions became more accurate. However, variance predictions at the extremes of the trajectory were still overestimated, and residuals showed a systematic pattern over the lactation period (Jamrozik et al., 1996). A low flexibility of the lactation function (Kettunen et al., 1998) and unequal weighting of data points with relatively more weight towards the

extremes of the lactation period (Meyer, 1998) were suggested to cause such bias.

To assess the order of fit needed for modeling the underlying structure in the data sufficiently, one could use the maximum likelihood test (Kirkpatrick et al., 1990). In general, the likelihood improved steadily with the order of fit (Meyer, 1998; Olori et al., 1999; Pool and Meuwissen, 1999; Van der Werf et al., 1998). However, for breeding value estimation, the accuracy and fluctuation of predictions is more important (Pool and Meuwissen, 2000). The same order has been suggested (Olori et al., 1999, Pool and Meuwissen, 1999) for both the genetic and environmental covariance matrices to ensure that both curves had equal flexibility. The RRM estimates have often (Kettunen et al, 1998; Pool and Meuwissen, 2000; Rekaya et al., 1999; Van der Werf et al., 1998) been compared with estimates from multiple-trait analyses. Although the multiple-trait analyses might be prone to uncertainties in the data because of lack of smoothing and modeling of different fixed effects, it should indicate the expected overall shape of the RRM. Eigenvalues of the genetic (co)variance matrix were calculated to indicate the relative impact and biological meaning of the successive orders (Meyer, 1998; Olori et al., 1999; Van der Werf et al., 1998).

Choices made for the RRM used in this study were based on results from earlier work. The order of fit needed to describe the lactation curve was investigated in a phenotypic RRM study (Pool and Meuwissen, 1999). A fifth-order Legendre polynomial was found to be sufficient (i.e., with six random regression coefficients) but up to a seventh-order of fit was estimable. However, further work (Pool and Meuwissen; 2000) showed that when only complete lactations were used for parameter estimation, one order less could be fitted without significantly reducing the goodness-of-fit. Also, a correction for heterogeneous variance over DIM allowed a reduction, but the overall computing time increased and, therefore, the latter was not implemented in this study. Thus, more accurate predictions were achieved when higher order polynomials were used (Pool and Meuwissen, 1999) and when only complete lactation records were included for the parameter estimation (Pool and Meuwissen, 2000) in a phenotypic Legendre polynomial TDM study. To distinguish the fit of different polynomial orders criteria as the shape of the covariance and correlation structure predicted versus that observed for the data, and the mean square error for prediction of missing records for different patterns of deleted records were used.

The aim of this study was to estimate and compare genetic and permanent environmental parameters of Legendre polynomials in a genetic RRM up to a fifth order of fit, by using a large data set of only complete lactations for first parity dairy cows in the Netherlands. In order to determine the order of fit needed (i.e., sufficient goodness-of-fit) the covariance and correlation structures predicted for both the genetic and permanent environmental components for different orders of fit were compared with those obtained from bivariate analyses.

MATERIALS AND METHODS

Data

In total, a data set was available for 2.2 million first-lactation records of Dutch Holstein-Friesian cows registered between July 1990 and December 1996. Edits were for age at calving (22 to 32 mo), breed (≥50% Holstein-Friesian), both parents known and test-day records from d 5 until 335. Milk recording frequency varied from weekly to 3-, 4- and 6-wk schemes between farms. Only complete lactations were selected to avoid any implicit interpolation or extrapolation in the model (Pool and Meuwissen, 2000). A complete lactation was considered to have a minimum of six milk recordings, an average test-day interval of a maximum 50 d, at least one test-day record at or before d 80, and one at or after d 280. In total, 14% of the lactation records were incomplete. The edited data contained 14.7 million test-day records on 1,427,848 first lactations from 20,659 herds with over 1.1 million herd test dates and sired by 7,369 bulls.

To obtain a smaller, more balanced and informative data set of approximately 20,000 lactations, restrictions were set to a minimum of 10 test-day records per herd test date and to animals with at least nine paternal half-sibs in the data set. The final data set contained 254,431 test-day records of 23,700 first-lactation records with an average test-day milk yield of 22.9 kg and a standard deviation of 5.3 kg. Lactation records selected were realized on 475 farms and included 14,069 herd test dates. The selected animals, sired by 262 bulls, were assumed to be a random sample from the Dutch dairy cattle population. Pedigree information was obtained from the national database. Animals not contributing connections (i.e., both parents unknown and only one offspring) were excluded. The final pedigree contained in total 63,853 entries, which were the offspring of 4,030 sires.

Model

Test-day records were modeled with Legendre polynomials (Kirkpatrick et al 1990; 1994) of different orders of fit [LEG(m)]. Parameters were estimated up to a fifth order of fit (i.e.,12 random regression coefficients per cow, six for the genetic component and six for the permanent environmental component). The matrix notation of the model is:

$$\text{LEG(m)}: \qquad \mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e} \qquad [1]$$

where, $\mathbf{y}$ = (n × 1) vector with test-day milk yields with n = number of observations; $\mathbf{b}$ = [μ; **ys**; **age**; **cDIM**; **HTD**]' = vector with fixed effects, where μ = the overall mean, **ys** = year season of calving (classes of 3 months within year), **age** = age at calving (age classes of 4 months), **cDIM** = weekly classes for days in milk, to model the average lactation curve, and **HTD** = herd test date effect; u = vector with ω random regression coefficients per animal

($k_{(\omega)}$) for the genetic effects of all animals, where $\omega = m + 1$, with m = order of fit; **p** = vector with ω random regression coefficients ($l_{(\omega)}$) for the permanent environmental effects of animals with test-day records; **e** = vector of residual effects; **X** = incidence matrix for the fixed effects; **Z** and **W** = incidence matrices for the genetic and permanent environmental effects, and **Z** is partitioned as [**Z₁ Z₂**], where **Z₁**=0 refers to the animals without records, and **Z₂** refers to the animals with records. The order of fit, m, was equal for the genetic and permanent environmental part; therefore, **Z₂ = W = T Λ**, where **T** = (n × ω) matrix with row vectors of size ω with standardized DIM (ranging from –1 to 1) to the power equal to the following order of fit (0… m). **Λ** = a (ω by ω) matrix with the polynomial coefficients on the Legendre scale (Kirkpatrick et al., 1990).

The (co)variance structure modeled for **u** is Var(**u**) = **A** ⊗ **G**, where **A** = additive genetic relationship matrix, ⊗ = Kronecker product function, and **G** = var($k_{(\omega)}$) = additive genetic covariance matrix of the genetic random regression coefficients. Similarly, Var(**p**) = **I** ⊗ **P**, where **I** = identity matrix, and **P** = var($l_{(\omega)}$) = permanent environmental covariance matrix of the random regression coefficients and describes the permanent environmental component of a lactation for a cow. The residual variance structure (σ_e^2) was assumed diagonal and constant over DIM.

Parameter Estimation

Variance components were estimated for a RRM with Legendre polynomials up to a fifth order of fit [LEG(m); m = 0… 5]. Because of the relative large data set, Bayesian inference using Gibbs sampling (Gelfand and Smith, 1990; Geman and Geman, 1984; Smith and Roberts, 1993) was implemented. The conditional distribution of the data was assumed to be multivariate normal

$$\mathbf{y}|\mathbf{b,u,p},\ \sigma_e^2 \sim N(\mathbf{Xb + Zu + Wp, I}\,\sigma_e^2) \qquad [2]$$

Gibbs samples were computed using the architecture of an iterative BLUP scheme according to Gauss-Seidel for solving the mixed-model equations [see (Janss and de Jong, 1999)]. In each round, elements of the vectors **b** were sampled and for **u** and **p** blockwise per animal from the full conditional posterior distributions

$$b_i|\mathbf{b}_{-i},\mathbf{u,p},\sigma_e^2,\mathbf{y} \sim N(\mathbf{x}_i'(\mathbf{y-X}_{-i}\mathbf{b}_{-i}\mathbf{-Zu-Wp})/n_i;\ \sigma_e^2/n_i) \qquad [3]$$

$$u_i|\mathbf{u}_{-i},\mathbf{p,G,P},\sigma_e^2,\mathbf{y} \sim N(\ [\mathbf{z}_i{}^{,}\mathbf{y}-\mathbf{z}_i'\mathbf{Xb}-(\mathbf{z}_i'\mathbf{Z}_{-i}+\mathbf{A}^{ii}\mathbf{G}^{-1}\sigma_e^2)\mathbf{u}_{-i}-(\mathbf{z}_i'\mathbf{W}_i+\mathbf{P}^{-1}\sigma_e^2)\mathbf{p}];\mathbf{B}_i^{-1}\sigma_e^2) \qquad [4]$$

$$p_i|\mathbf{u,p}_{-i},\mathbf{G,P},\sigma_e^2,\mathbf{y} \sim N(\ [\mathbf{w}_i'\mathbf{y}-\mathbf{w}_i'\mathbf{Xb}-(\mathbf{w}_i'\mathbf{Z}_i+\mathbf{A}^{ii}\mathbf{G}^{-1}\sigma_e^2)\mathbf{u}-(\mathbf{w}_i'\mathbf{W}_{-i}+\mathbf{P}^{-1}\sigma_e^2)\mathbf{p}_{-i}];\mathbf{D}_i^{-1}\sigma_e^2) \qquad [5]$$

where n_i = number of observations in fixed effect class i, $\mathbf{B}_i = (\mathbf{z}_i'\mathbf{z}_i + \mathbf{A}^{ii}\mathbf{G}^{-1}\sigma_e^2)$, $\mathbf{D}_i = (\mathbf{w}_i'\mathbf{w}_i + \mathbf{A}^{ii}\mathbf{G}^{-1}\sigma_e^2)$, and $\mathbf{u}_i$ and $\mathbf{p}_i$ = vectors with genetic and permanent environmental effects per animal. Blockwise sampling was implemented by decomposing the matrix of animal parameters into a lower and upper triangular matrix (i.e., LU-decomposition). Next, variance components were updated from the quadratic forms. The update of σ_e^2 was sampled, assuming an uniform prior distribution, from the full conditional posterior distribution

$$\sigma_e^2 | \mathbf{b}, \mathbf{u}, \mathbf{p}, \mathbf{y} \sim SSE / \chi_v^2 \qquad [6]$$

which is an inverted chi-square distribution where SSE = $\mathbf{e}'\mathbf{e}$ ($\mathbf{e}$ follows from [1]), and v = n-2 degrees of freedom. For $\mathbf{G}$ and $\mathbf{P}$, the full conditional posterior distributions were inverted Wishart (IW) distributed with dimension ω of $\mathbf{G}$ and $\mathbf{P}$ (i.e., order of fit+1). Uniform priors were assumed (Wang et al., 1994); therefore, the full conditional posterior distributions for $\mathbf{G}$ and $\mathbf{P}$ are:

$$\mathbf{G} | \mathbf{u} \sim IW(\mathbf{SSG}^{-1}, v) \qquad [7]$$
$$\mathbf{P} | \mathbf{p} \sim IW(\mathbf{SSP}^{-1}, v) \qquad [8]$$

where v = n-(ω+1) degrees of freedom and scaling parameters are

$$\mathbf{SSG} = \begin{bmatrix} \mathbf{u}_0'\mathbf{A}^{-1}\mathbf{u}_0 & \cdots & \mathbf{u}_m'\mathbf{A}^{-1}\mathbf{u}_0 \\ \vdots & \ddots & \vdots \\ \mathbf{u}_m'\mathbf{A}^{-1}\mathbf{u}_0 & \cdots & \mathbf{u}_m'\mathbf{A}^{-1}\mathbf{u}_m \end{bmatrix} \text{ and } \mathbf{SSP} = \begin{bmatrix} \mathbf{p}_0'\mathbf{p}_0 & \cdots & \mathbf{p}_m'\mathbf{p}_0 \\ \vdots & \ddots & \vdots \\ \mathbf{p}_m'\mathbf{p}_0 & \cdots & \mathbf{p}_m'\mathbf{p}_m \end{bmatrix}.$$

Samples were obtained from a ω-dimensional Wishart distribution [$W_\omega(SS,v)$] according to a procedure described by Sorensen (Sorensen, 1997) and were subsequently inverted to yield samples of an inverse Wishart distribution (Sorensen, 1997) using a LU-decomposition. The marginal posterior means obtained in this procedure were used as estimates for the variance components. The Gibbs sampler was run until the effective chain size ($\tilde{\psi}$) was approximately 50 independent samples for most variance components. $\tilde{\psi}$ was computed as $\hat{\gamma}(0) / \widehat{Var}(\hat{\alpha})$, where $\hat{\gamma}(0)$ = lag(0)-autocovariance which is a measure for the amount of covariance between subsequent samples, and $\widehat{Var}(\hat{\alpha})$ = estimated variance of the Monte Carlo variance estimator, which is the sampling variance [see Sorensen, (1997) for details]. Burn-in (determined graphically), total chain length, and effective chain size are given in Table 1 for the different orders of fit.

Model Comparison

Parameter estimates and covariance structures predicted by the different Legendre polynomial RRM were compared with those from a multiple-trait analysis using ASREML (Gilmour et al., 1999). In the multiple-trait analysis, the lactation trajectory (d 5 to 305) was split into 10 periods of 30 d, and (co)variance components were estimated by 45 bivariate analyses. The fixed effects of year-season at calving and age at calving were accounted for as in the RRM, but herd-year-season classes of 3 mo were used instead of herd test date effects. For the genetic and permanent environmental covariance matrices of the polynomial coefficients, eigenvalues were calculated to quantify the relative importance of each order.

RESULTS

Model Parameters

Burn-in and effective chain length increased strongly with the order of fit to reach approximately 50 independent samples (Table 1). Effective chain size for each variance component was at least 50 independent samples long, except for $k_{5(4,4)}$, which was 40 (where $k_{m(i,j)}$ = covariance estimate between the genetic random regression coefficients i and j in an RRM with order of fit m).

Table 1. Burn-in, total chain length, and effective chain size for random regression models with different Legendre polynomial orders of fit m [LEG(m)]

Model	Number of chains	Burn-in	Length of all chains in total	Range in effective chain size[1] (minimum - maximum)		
LEG(0)	2	2,000	196,901	177	-	192
LEG(1)	2	3,250	316,901	240	-	296
LEG(2)	2	2,600	899,775	528	-	777
LEG(3)	3	4,000	356,186	96	-	302
LEG(4)	2	14,000	499,106	71	-	437
LEG(5)	2	45,000	346,418	40	-	737

[1] Effective chain size was calculated as the lag-0-autocovariance divided by the variance of the Monte Carlo variance estimator (24) for the total chain length. Minimum and maximum is the effective total chain size for the variance component estimate with the lowest and highest number of independent samples, respectively.

Residual variance estimates decreased steadily with the polynomial order of fit (Table 2). Although, the decrease in residual variance seemed to stabilize for the higher orders, it was still 8.9% from LEG(2) to LEG(3) and 5.4% from LEG(3) to LEG(4). Covariances between

the random regression coefficients are presented as correlations in Table 3 (genetic correlations below diagonal and phenotypic correlations above diagonal). In all models,

Table 2. Estimates of residual variances (σ_e^2) and posterior standard deviations (in brackets) of milk yield (in kg^2) among DIM modeled for random regression models with different Legendre polynomial orders of fit m [LEG(m)].

Model	σ_e^2	(posterior st.dev)	Model	σ_e^2	(posterior st.dev)
LEG(0)	4.646	(0.014)	LEG(3)	2.601	(0.010)
LEG(1)	3.444	(0.011)	LEG(4)	2.460	(0.010)
LEG(2)	2.856	(0.010)	LEG(5)	2.364	(0.010)

Table 3. Correlation estimates between covariance function coefficients for the genetic (below diagonal) and permanent environmental component (above diagonal) from a test-day model with Legendre polynomials of different orders of fit m [LEG(m)].

LEG(2)

	$c_{0(2)}$[1]	$c_{1(2)}$	$c_{2(2)}$
$c_{0(2)}$	-	0.00	-0.04
$c_{1(2)}$	-0.02	-	-0.01
$c_{2(2)}$	-0.61	-0.02	-

LEG(4)

	$c_{0(4)}$	$c_{1(4)}$	$c_{2(4)}$	$c_{3(4)}$	$c_{4(4)}$
$c_{0(4)}$	-	0.01	-0.06	0.02	-0.14
$c_{1(4)}$	-0.02	-	-0.01	0.11	0.05
$c_{2(4)}$	-0.64	-0.02	-	-0.18	-0.03
$c_{3(4)}$	0.46	-0.25	-0.45	-	-0.32
$c_{4(4)}$	-0.33	0.36	0.35	-0.39	-

LEG(3)

	$c_{0(3)}$	$c_{1(3)}$	$c_{2(3)}$	$c_{3(3)}$
$c_{0(3)}$	-	0.02	-0.02	0.07
$c_{1(3)}$	0.01	-	-0.02	0.12
$c_{2(3)}$	-0.62	-0.07	-	-0.10
$c_{3(3)}$	0.47	-0.25	-0.42	-

LEG(5)

	$c_{0(5)}$	$c_{1(5)}$	$c_{2(5)}$	$c_{3(5)}$	$c_{4(5)}$	$c_{5(5)}$
$c_{0(5)}$	-	0.03	-0.05	0.07	-0.12	0.11
$c_{1(5)}$	-0.01	-	-0.02	0.04	-0.00	-0.14
$c_{2(5)}$	-0.62	-0.05	-	-0.20	-0.09	-0.02
$c_{3(5)}$	0.47	-0.32	-0.38	-	-0.40	-0.17
$c_{4(5)}$	-0.36	0.32	-0.33	-0.66	-	-0.27
$c_{5(5)}$	0.28	-0.40	-0.07	0.50	-0.82	-

[1] $c_{j(m)}$ = random regression coefficient j in model LEG(m) for either the genetic or the permanent environmental component in the (co)variance matrix.

covariance matrices were positive definite for both the genetic and permanent environmental parts. Correlations between the random regression coefficients i and j in LEG(m) with order of fit m ranged for the genetic component ($r_{k_i k_j (m)}$) from -0.82 for $r_{k_4 k_5 (5)}$ to 0.50 for $r_{k_3 k_5 (5)}$ and for permanent environmental ($r_{l_i l_j (m)}$) part from –0.40 for   to 0.12 for . In general, correlations were stronger for the genetic component, especially between the high-order coefficients.

(Co)variance Component Estimates

Genetic and permanent environmental variances were calculated for each day along the lactation trajectory from the estimated covariance function coefficients. The permanent environmental and residual variances (summed together) were high at the beginning and end of lactation and lower in between (Figure 1). For clarity, not all orders of fit where presented in the figures, but only those really differing from each other. However, all models, except LEG(0) and LEG(1), predicted variances with a similar shape, as was observed from the bivariate estimates. The goodness-of-fit (i.e., the predicted shape of variances over DIM compared with the bivariate estimates) improved with the order of fit, although the absolute level of variance estimates was slightly lower. The latter is probably due to better correction of the fixed effects in RRM compared with the bivariate model. When the complete covariance
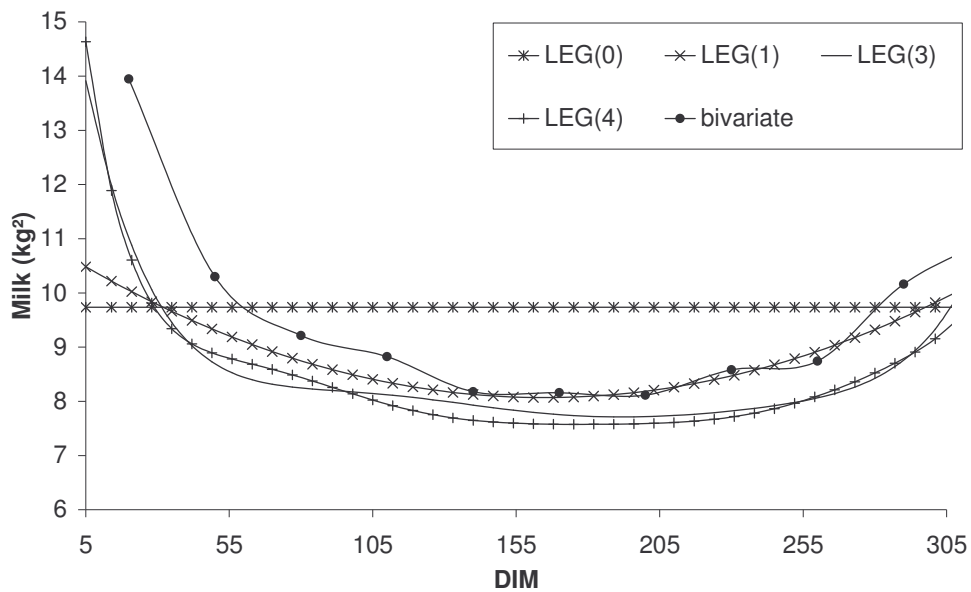

Figure 1. Permanent environmental and residual variances (summed together) of milk yield over DIM predicted with Legendre polynomials for different orders of fit m [LEG(m)] by a test-day model compared to those obtained from bivariate analyses.
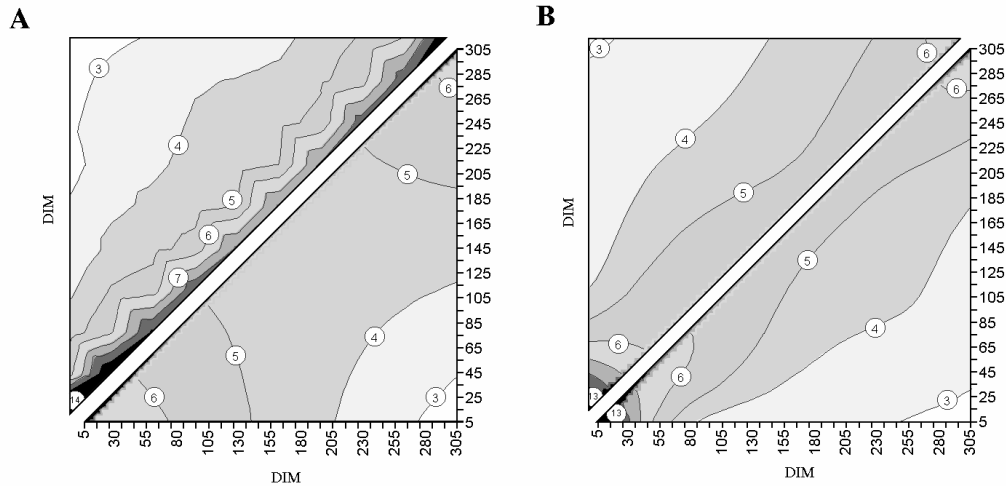
Figure 2. Stacked areas with the permanent environmental covariance structure for milk yield over DIM predicted with Legendre polynomials for different orders of fit m [LEG(m)] by a test-day model compared with those obtained from a multiple-trait model (bivariates). Units are given on the contour lines and expressed in kg^2. left graph (A): Bivariate (upper triangle) and LEG(1) (lower triangle) and right graph (B): LEG(3) (upper triangle) and LEG(4) (lower triangle).

structures were plotted as stacked areas (Figure 2), the observed shape (bivariate) seemed different from LEG(1) and was not modeled with sufficient accuracy until LEG(4) was used (not all results presented). Although differences between LEG(3) and LEG(4) were small, based on the predicted covariances at least a fourth order polynomial [LEG(4)] was needed to model the permanent environmental covariance structure. Predictions of genetic variances over DIM (Figure 3) varied considerably more between models. The shape of the bivariate estimates was not very smooth because of the 30-d intervals, and they showed an unexpected drop around d 105. The lower-order models, LEG(0) and LEG(1), predicted a basically different shape, which implied that a higher-order polynomial regression (i.e., LEG(3) or higher) was necessary for a sufficient fit of the genetic covariance structure over the whole trajectory in an RRM. In general, the bivariate genetic variances were lower than the genetic covariances for the RRM. This result may be because the bivariate genetic covariance estimates were actually estimating the average covariance between the DIM of a 30-d period, which is lower than the genetic variance at a particular DIM as predicted by the RRM. Note that LEG(0) estimated the average genetic covariance over all DIM and, therefore, yielded the lowest genetic variance (Figure 3). Complete genetic covariance structures (Figure 4) showed

Figure 3. Genetic variances of milk yield over DIM predicted with Legendre polynomials for different orders of fit m [LEG(m)] by a test-day model compared with those obtained from bivariate analyses.

that LEG(1) predicted a different shape than observed (bivariate). For the higher orders, bias of the bivariates was largest for predictions of covariances along the diagonal for days not far apart and small elsewhere. When comparing LEG(3) and LEG(4), LEG(4) fit the shape of the covariance structure slightly better in the beginning of the lactation.

Heritability estimates along the lactation trajectory (Figure 5) showed similar shapes as for the genetic variation but were less extreme at the beginning and end of the trajectory because of higher permanent environmental variances. Bivariate estimates varied from 0.21 to 0.43. The heritability of the repeatability model [i.e., LEG(0)] was 0.31 and was close to the value currently used in the lactation model, indicating that the RRM did not overestimate the heritability. For the higher orders of fit [LEG(2) - LEG(5)], heritability varied from 0.20 to 0.46. Overall, model LEG(3) and higher resembled the bivariate estimates well, although the absolute level was slightly higher, which was probably caused by averaging of the covariances between DIM for the bivariates, and better correction for the correlations among DIM within the RRM.

Eigenvalues of Covariance Matrices

Eigenvalues (Table 4) for the genetic and permanent environmental matrices of random regression coefficients did not vary much for the different orders, except the first eigenvalue. For the genetic part, the first three eigenvalues explained over 98% of the variation, but for the

A

B

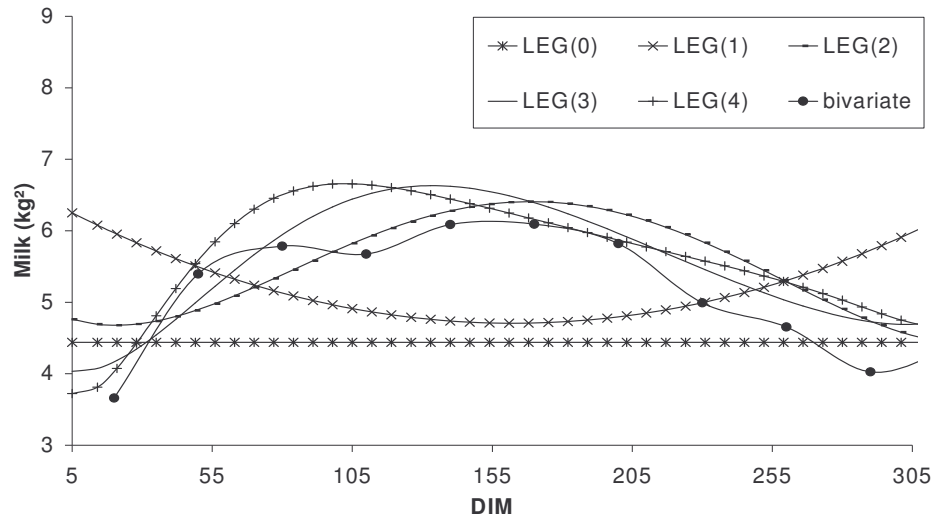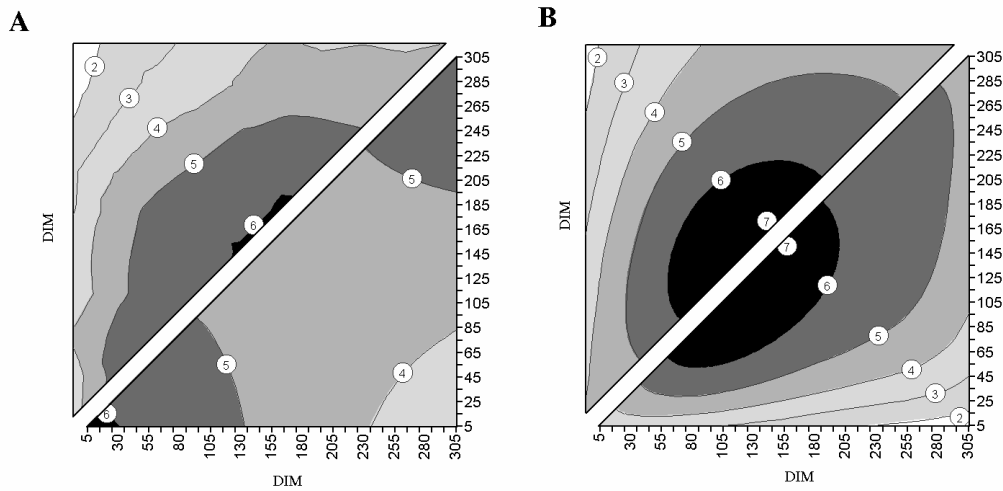Figure 4.   Stacked areas with the genetic covariance structure for milk yield over DIM predicted with Legendre polynomials for different orders of fit m [LEG(m)] by a test-day model compared with those obtained from a multiple-trait model (bivariates). Units are given on the contour lines and expressed in kg^2. Left graph (A): Bivariate (upper triangle) and LEG(1) (lower triangle) and right graph (B): LEG(3) (upper triangle) and LEG(4) (lower triangle).
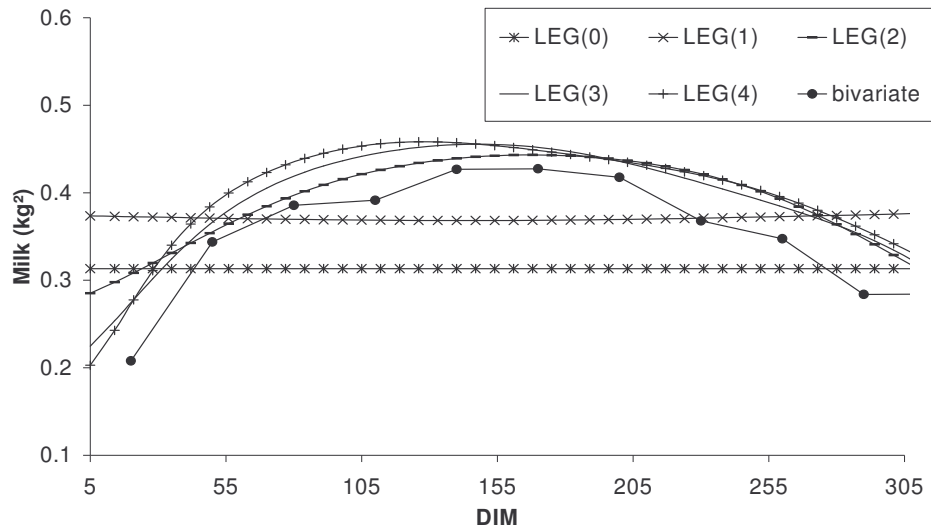

Figure 5.   Heritability estimates for milk yield over DIM predicted with Legendre polynomials for different orders of fit m [LEG(m)] by a test-day model compared with those obtained from bivariate analyses.

(zero-th order) for permanent environment decreased with the order of fit of the model. permanent environmental part, four eigenvalues were needed to explain over 98%; five were needed to explain over 99%. Hence, LEG(3) or LEG(4) was needed to fit the permanent environment appropriately [i.e., over 99% of the variance was explained by model LEG(5)]. Because the order of fit of genetic covariances should be equal to that of the permanent environment (Pool and Meuwissen, 1999), LEG(3) or LEG(4) is also needed for the genetic effects (despite that Table 4 suggests that it might be modeled by a lower-order Legendre polynomial)

Table 4. Eigenvalues and relative proportions (in brackets) for the genetic and permanent environmental random regression coefficient matrices with different Legendre polynomial orders of fit m [LEG(m)]

Model order	Zero-th	First	Second	Third	Fourth	Fifth	sum[1]
Genetic eigenvalues (proportion)							
LEG(1)	9.42 (89.3)	1.13 (10.7)					10.55 (93.3)
LEG(2)	9.58 (87.7)	1.07 (9.8)	0.28 (2.5)				10.93 (96.6)
LEG(3)	9.68 (87.8)	1.03 (9.4)	0.26 (2.3)	0.06 (0.5)			11.03 (97.5)
LEG(4)	9.77 (87.0)	1.10 (9.8)	0.26 (2.3)	0.06 (0.5)	0.05 (0.4)		11.23 (99.3)
LEG(5)	9.81 (86.8)	1.08 (9.5)	0.26 (2.3)	0.11 (1.0)	0.04 (0.3)	0.01 (0.1)	11.31 (100.)
Permanent environmental eigenvalues (proportion)							
LEG(1)	9.25 (84.4)	1.71 (15.6)					10.97 (89.0)
LEG(2)	9.06 (77.7)	1.75 (15.0)	0.85 (7.3)				11.67 (94.6)
LEG(3)	9.15 (74.8)	1.82 (14.8)	0.83 (6.8)	0.44 (3.6)			12.24 (99.3)
LEG(4)	8.99 (73.4)	1.82 (14.9)	0.84 (6.8)	0.43 (3.5)	0.17 (1.4)		12.25 (99.4)
LEG(5)	9.04 (73.3)	1.77 (14.4)	0.84 (6.8)	0.42 (3.4)	0.18 (1.4)	0.07 (0.7)	12.33 (100.)

[1] Sum of m eigenvalues for the model LEG(m) and in brackets the relative amount of variance explained indexed to LEG(5)

DISCUSSION

For the implementation of a RRM in the genetic evaluation of dairy cattle, it is important that breeding values are estimated accurately and that predictions do not fluctuate if information accumulates. Therefore, the goodness-of-fit of a RRM (i.e., the minimum order needed to model the observed variance in the data with sufficient accuracy by a covariance function) should be investigated carefully. Although this would suggests high orders of fit,

such models could lead to incorrect estimates because of overparameterization (Jamrozik and Schaeffer, 1997; Kettunen et al., 1998); moreover, the feasibility of the RRM depends on the order of fit because of limited computing resources. Therefore, the order (i.e., the number of parameters to be estimated per animal) should be kept as low as possible. In an earlier phenotypic study (Pool and Meuwissen, 2000), a third-order polynomial RRM was sufficient if complete lactations were used for parameter estimation and a correction of heterogeneous variances over DIM was applied. Without those two restrictions, a fifth-order polynomial covariance function was required. Although higher orders of fit (i.e., up to a seventh-order) were estimable, the goodness of fit improved hardly anymore. However, in a genetic RRM, the number of parameters is doubled when the random part of a lactation curve is modeled by two polynomial random regression functions, one for the genetic part and one for the permanent environmental part. To ensure that both functions equally well fit (i.e., to avoid problems of permanent environmental variances being fitted by the genetic curve and vise versa) the same order of fit was used for both effects. Further, any implicit extrapolation was avoided by selecting only complete lactations. Discarding the incomplete lactations (14%) might have introduced a selection bias in the data (e.g., might have been due to poorly producing cows that did not get the chance to complete the lactation). However, this possible selection bias seemed to have little effect on the observed variances for daily milk yields and yielded even better estimates for predictions of missing records (Pool and Meuwissen, 2000).

Preliminary results from 8000 lactations, using ASREML, were inconsistent and indicated that more lactations (i.e., more informative information) should have been used. Therefore a relatively large data set of 23,700 complete lactations was created. Although, selection for at least 10 observations per herd test date might have favored lactations from large farms, and selection of at least nine paternal half-sibs might have favored evaluated bulls, we assumed that the data set was a representative sample of the Dutch cattle population. All 23,700 first lactations were realized on 457 herds and the cows selected were offspring of 262 sires (69% had up to 50 daughters, and 81% had up to 100 daughters). By selecting those animals the information contents of the data increased, by avoiding small fixed effect classes and ensuring large enough offspring groups to improve estimation of the animal effects.

With high orders of fit and a large data set, the memory requirement of deterministic variance component estimation programs based on direct solving of the mixed-model equations was enormously. Therefore, Gibbs sampling was used instead and needed less than 40 Mb of memory although computing time increased remarkable. With flat priors, no assumptions have to be made about prior information, and parameters will be estimated fully from the information content of the data. The estimates from Gibbs sampling resemble maximum likelihood estimates, because of, in a Bayesian analyses with flat priors for variance components, the modes of the joint posterior distribution $f(\mathbf{G},\mathbf{P},\sigma_e^2|\mathbf{y})$ equals the REML

estimates (Harville, 1974). However, we used the marginal posterior means in the Gibbs analyses, because differences between posterior means and joint modes are negligible in large analyses. Therefore, posterior means reported for the Gibbs analyses are comparable to the REML solutions.

On first sight the bivariate estimates showed slightly different patterns (i.e., lower level and less smoothed) as the RRM even with higher orders of fit and might be explained by the way it was analyzed. The 30-d intervals used in the bivariate analyses resulted in some averaging over DIM and lowered predictions for the (co)variance and correlation estimates, which was especially apparent for days close together. More data and smaller intervals would smooth the shape for the bivariate estimates and overcome the problem. Also the different fixed-effect corrections in the bivariate analyses (i.e., herd-year-seasons instead of herd test date and no correction for DIM within the 30-d period) may have influenced the level of bivariate estimates. The RRM might include different fixed-average lactation curves to observe the level of production better for different groups of cows.

The genetic and permanent environmental variance estimates realized in this study were of the same order as in the literature (Olori et al., 1999; Rekaya et al., 1999). Results were very similar to Rekaya et al. (1999), although they described slightly higher variance estimates at the extremes of the lactation curve and a flatter heritability curve. That is, the curve was higher at the beginning and end of lactation and was lower in between for a fifth-order regression on DIM. Genetic variances described by Olori et al. (1999) were of a higher level and increased toward the end of lactation. In contrast, our results for genetic variance were highest in the middle of lactation, as observed for the bivariate estimates. Averaging within the bivariate estimates and accounting for correlations among test days in the RRM, resulted in higher heritability estimates for daily test-day records in the RRM. Heritability of lactation yield was, as expected, even higher, but comparable with values reported in literature for first lactations (Janss and de Jong, 1999) and suggest that the RRM did not overestimate the heritability.

The choice of the required order of fit was based on the following.
1. Residual variances (Table 2). Those decreased steadily with the order of fit but were less than 5% when substituting LEG(4) by LEG(5). Therefore the improvement with higher orders of fit was limited, and the reduction of residual variance might be mainly due to fitting irregularities in the data.
2. Genetic and permanent environmental variances (Figures 1 and 3). Due to more flexible curves, LEG(3) and LEG(4) seemed to fit the genetic and permanent environmental variances better compared to the lower orders of fit.
3. Genetic and permanent environmental covariances (Figure 2 and 4). The fit of LEG(4) has the most similar shape as the bivariate estimates for permanent environmental covariances

59

observed in the data. Compared to LEG(3) and LEG(4), which modeled similar shapes as observed for the bivariate genetic covariances, the shape fitted by model LEG(1) was structurally different.

4. Eigenvalues for the genetic and permanent environmental covariance function matrices (Table 4). A sufficiently large proportion of the variances observed for test-day records in the data was explained by LEG(3) and LEG(4) based on the eigenvalues. And, the relative higher value of the permanent environmental eigenvalues indicated that the permanent environmental effect needed to be modeled with more, higher orders of fit than necessary for the genetic component.

Thus, LEG(3) or LEG(4) seemed to yield a sufficient fit of the covariance matrices based on these criteria. In previous work (Pool and Meuwissen, 2000), it was found that an accurate prediction of missing records tended to equal the highest order. Therefore, our recommendation is to use a fourth-order polynomial [LEG(4)] for both the genetic and permanent environmental effects, such that the model is equally well equipped to model both effects (Olori et al, 1999; Pool and Meuwissen, 1999). However, the relatively small eigenvalues for higher orders indicated that a simpler covariance function of reduced rank might be based on the eigenvectors pertaining to the highest eigenvalues. When all eigenvalues with a relative value of less than 2% are set to zero, the genetic covariance matrix is of rank three and for permanent environment of rank four. Thus, it seems that the genetic covariance matrix can be modeled simpler than permanent environment and that the number of parameters to be estimated per cow can be reduced while maintaining the high order Legendre polynomial in a RRM. Computationally a fourth-order RRM was feasible, but for further development of the model into a multiple lactation model and especially into a multiple lactation and multiple-trait RRM the number of parameters will increase considerably and a further reduction of the number of parameters will be necessary.

——————————

Stepwise reducing the number of fitted parameters in multiple-trait lactation random regression test-day models.

(M. H. Pool[a,b], and T.H.E. Meuwissen[b])

[a]   Wageningen Institute of Animal Science (WIAS).

[b]   Department of Genetics and Reproduction. Institute of Animal Health and Science
(ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

ABSTRACT

The number of parameters to be estimated per animal in multiple-lactation random regression test-day models can be halved when the ranks of covariance functions were reduced step by step. Based on fourth order Legendre polynomials and three lactation traits, the covariance function in a full multiple-trait model would be of dimension 15 (3×5) for both the genetic and permanent environmental part (i.e., 30 coefficients per animal). With data from 23,700 animals (63,583 pedigree entries) over 1,3 million equations had to be solved. Such a large model is not very parsimonious and computationally hard to solve, reducing the number of parameters without giving in to the goodness of fit is preferred.

A stepwise-reduced rank procedure was investigated and illustrated by two approaches, firstly by including information of different parities stepwise into the model (INCL-x), and secondly by running the model separately for parities and combining those after reducing the ranks (LACT-x). In each step, the ranks of the covariance functions were reduced (as much as possible) by setting the eigenvalues with a cumulative sum of less than 2% equal to zero. The genetic and environment rank was respectively 9 and 4 orders for INCL-x (reduction of 17 parameters), and 10 and 5 for LACT-x (reduction of 15 parameters). In INCL-x, first parties obtained reduced weight. More first parity records gave a better fit of first and second parities at the expense of third parities. Overall approach LACT-x yielded the best fit and was recommended for extension into a multiple-trait and lactation model for milk, fat, and protein.

INTRODUCTION

Milk production of a dairy cow is variable over days in milk (**DIM**). In general, daily milk yield increases until peak (around day 60) and decreases steadily after that. However, the level and shape of the production curve along the lactation trajectory differs between animals. Unlike in a lactation model, which only includes level of production for breeding value estimation, a test-day model (**TDM**) can account for the variability in both the level and shape

of the lactation curve. The modeling of individual test-day records in a TDM instead of 305d productions in a lactation model allows the TDM to correct for the effect of test-date, number of test-days, interval between test-days, and ordering of test-day records (Swalve, 1995); thus can prediction the mean production level more precise. Theoretically, the shape of a lactation curve should be modeled the best by considering each test-day as a different trait within a multiple-trait TDM. However, such a model is not very parsimonious and computationally demanding. Therefore an approach that describes the shape of the lactation curve by modeling daily productions over DIM using random regression functions (Schaeffer and Dekkers, 1994) is more appealing. Many functions have been investigated to model individual lactation curves (Guo and Swalve, 1997a; Jamrozik et al., 1997a; Pool and Meuwissen, 1999; Ptak and Schaeffer, 1993). Function based models, that describe the change of variances and covariances over time are known as covariance function models (**CF**, Kirkpatrick et al., 1994). In the case of linearized random regression functions the covariance matrices can be estimated directly from the data (Meyer and Hill, 1997) by the random regression approach (RR, Schaeffer and Dekkers, 1994); which is shown to be equivalent to CF (Meyer, 1998; Van der Werf et al., 1998).

Many studies have reported parameter estimates for a single trait TDM (Jamrozik et al., 1996; Kettunen et al., 1998; Meyer et al., 1989; Olori et al., 1999; Pool et al., 2000; Pander et al., 1992; Rekaya et al., 1999). In an earlier study based on a phenotypic RR TDM with only first parity test-day records (Pool and Meuwissen, 1999) we showed that higher order Legendre polynomials (**LEG**) were required to fit the lactation curve sufficiently accurate; with at least a fourth order of fit [LEG(4)] (i.e., with five random regression coefficients to be estimated per animal). Based on the information contents of the data the parameter estimates improved clearly when the analyses were based on test-day records from only completed lactations (Pool and Meuwissen, 2000). At the same time, the deletion of records from incomplete lactations allowed a reduction of the sufficient order of fit with one order less. Although this improved the accuracy of the parameter estimates, variance predictions at the outer parts of the lactation period were still overestimated. To ensure equal flexibility for modeling of both, the genetic and permanent environmental covariances, it was suggested to model both effects with a function (Jamrozik et al., 1996; Kettunen et al., 1998). Preferably, with the same function, and of equal order of fit (Pool and Meuwissen, 1999; 2000), although it actually doubles the number of parameters to be estimated per animal.

Lactation information from an animal for different parities varies for both, the level and shape of the production curve, and is actually realized in subsequent but different periods. Therefore it seems that lactation information of different parities should not be considered as repeated traits but as different traits with independent measurement errors, such that one can

account also for the variability between parities. However, extension of a single lactation RR TDM into multiple-trait lactation RR TDM will increase the number of parameters drastically. Based on LEG(4) and for three parities, the number of parameters to be estimated per animal will expand to in total 30 (i.e., with a CF-matrix of dimension 15 for both the genetic and permanent environmental effects). Therefore one might run into problems due to overparameterization, and limited computing resources in models for parameter estimation but especially to solve the mixed model equations in models for routinely breeding value estimation. Using less sophisticated models or a smaller data set would solve computational problems, however the former may yield biased estimates, and the latter will yield increased sampling errors. Different approaches are described to estimate parameters with large TDM, e.g., a repeatability multiple-trait RR TDM (Rekaya et al., 1999), reduced rank multiple-trait TDM (Wiggans and Goddard, 1997), reduced rank RR TDM with CF estimated indirectly (Mäntysaari, 1999; Van der Werf et al., 1998; Veerkamp and Goddard, 1998) or directly (Meyer, 1998) from the data, but for all models the number of parameters to estimate is large. In general, the more sophisticated the models are the better the results seem to be, however if parameter estimates are biased or have high sampling variances, gains expected from the TDM may not be realized. As an alternative it was suggested by Misztal et al. (2000) to investigate a stepwise multiple-trait reduced rank procedure in order to reduce the number of parameters further. In comparison with other reduced rank approaches, the stepwise procedure gives the opportunity to reduce the rank of the CF for the genetic and permanent environmental effect independent of each other and does not depend on missing records.

The aim was to estimate CF parameters for first, second and third parity lactation test-day records with multiple-trait lactation RR TDM where the rank of the CF-matrices was reduced step by step. Multiple lactation records from an animal were treated as different but correlated traits, and modeled by a reduced number of parameters while maintaining the goodness of fit as much as possible. The procedure of stepwise reducing the rank of multiple-trait lactation RR TDM was described and illustrated by two approaches. Firstly by including information of multiple lactations stepwise to the RR TDM, and reducing the rank of the model after each step as much as possible. Secondly by estimating first single trait RR TDM for first, second and third lactations separately, reducing the rank of the CF-matrices, and combining those reduced rank models into one multiple-trait lactation RR TDM.

MATERIALS AND METHODS
Data

A data set of 498,724 test-day records from 23,700 first (253,448 records), 13,463 second (142,133 records), and 10,031 third parity lactations (103,143 records) was used. All lactations were from Holstein-Friesian cows born between November 1987 until September

1994. First parity lactation data was as described in Pool et al. (2000), and second and third parity lactation data was included, if available. Edits were for age at calving (first parity: 22 to 32 months, second: 33 to 50 months, and third: 45 to 67 months), breed ($\geq$ 50% HF), both parents known, and test-day records from day 5 until 335. All test-day records used were collected by the regular national milk recording system which varied in frequency between farms from weekly to 3-, 4-, and 6-weekly intervals. To avoid any implicit inter- and extrapolation in the model only complete lactations were used (Pool and Meuwissen, 2000); with a minimum number of six test-day records, an average test-day interval of at maximum 50 days, at least one test-day record at or before day 80, and one at or after day 280. Test-day records of animals that moved during the lactation were deleted. To ensure a more informative and balanced data set, first parity lactation test-day records were selected with the restriction of minimal 10 test-day records per herd test date, and from animals with at least 9 paternal half sibs in the data set [as applied in Pool et al. (2000)]. Average test-day milk yield was 22.9 kg with a standard deviation of 5.3 kg for first parity test-day records, 27.3 kg with a standard deviation of 8.1 kg for second parity data, and 29.1 kg with a standard deviation of 9.0 kg for third parity data. All lactations were realized on 490 farms. Animals with data records were offspring of 262 sires. The pedigree contained in total 63,853 entries that were the offspring off 4,030 sires.

Test-day Model

The multiple-trait lactation RR TDM was applied using LEG (Kirkpatrick et al., 1990; 1994) for describing the genetic and permanent environmental CF in first, second, and third parities. Based on previous results (Pool and Meuwissen, 1999), fourth order polynomials (five parameters for the genetic and five for the permanent environmental component) were suggested. The general model of analysis was:

$$\text{LEG}(m): \qquad \mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e} \qquad [1]$$

where, $\mathbf{y}$ = vector of test-day milk yields for all traits (of length $N_\bullet = \sum_{i=1}^{t} N_i$, and ordered by animal within trait; where N_i = number of observations for trait i); $\mathbf{b} = [\mu; \mathbf{ys}_t; \mathbf{age}_t; \mathbf{cDIM}_t; \mathbf{HTD}]'$ = vector with fixed effects, where μ = overall mean, $\mathbf{ys}_t$ = year season of calving (classes of 3 months within year and trait), $\mathbf{age}_t$ = age at calving (classes of 4 months within trait), $\mathbf{cDIM}_t$ = average lactation curve (i.e., weekly classes for days in milk within trait), and $\mathbf{HTD}$ = herd test date effects; $\mathbf{u}$ = vector with additive genetic effects per animal, where $m_\bullet = \sum_{i=1}^{t} m_i$ random regression coefficients [$\mathbf{k}_{(m_\bullet)}$] for all animals, and $\mathbf{p}$ = vector with random

regression coefficients [$\mathbf{l}_{(m_{t \cdot})}$] for the permanent environmental effects of animals with test-day records (m_t indicates the number of polynomial coefficients to describe trait t for $\mathbf{u}$ and $\mathbf{p}$ respectively. For simplicity of notation m_t was assumed equal for both effects but they actually do differ); $\mathbf{e}$ = vector of residuals for measurement errors. $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ = incidence matrices pertaining to $\mathbf{b}$, $\mathbf{u}$, and $\mathbf{p}$, respectively. $\mathbf{Z}$ and $\mathbf{W}$ can be partitioned into blocks per trait; $\mathbf{Z}_t$ and $\mathbf{W_t}$, with $\mathbf{Z} = \begin{bmatrix} \mathbf{Z}_{1(1)} & \cdots & \mathbf{Z}_{t(1)} \\ \mathbf{Z}_{1(2)} & \cdots & \mathbf{Z}_{t(2)} \end{bmatrix}$, and $\mathbf{W} = \begin{bmatrix} \mathbf{W}_1 \cdots \mathbf{W}_t \end{bmatrix}$, where $\begin{bmatrix} \mathbf{Z}_{1(1)} \cdots \mathbf{Z}_{t(1)} \end{bmatrix} = 0$ and refers to the animals without records for a trait, and $\begin{bmatrix} \mathbf{Z}_{1(2)} \cdots \mathbf{Z}_{t(2)} \end{bmatrix}$ refers to the animals with records for trait 1 to t. $\mathbf{Z}_{t(2)}$ and $\mathbf{W}_t$ are calculated as $\mathbf{S}_t \mathbf{\Lambda}_{tt}$ and are equal if the number of polynomials (m_t = order of fit +1) is equal for both the genetic and permanent environmental part. With $\mathbf{S}_t$ = (Nt by m_t) matrix of row vectors with scaled standardized days in milk (sDIM). $\mathbf{\Lambda}_{tt}$ = (m_t by m_t) matrix with the polynomial coefficients on the Legendre scale (Kirkpatrick et al., 1990). Note that each row vector in $\mathbf{S}_t$ is partitioned per trait as: $\mathbf{s}_i = \begin{bmatrix} \mathbf{s}_{i1} \cdots \mathbf{s}_{it} \end{bmatrix}$ with $\mathbf{s}_{it}$ = ($1 \times m_t$) row vector with sDIM (ranging from –1 to 1) to the power equal to the following order of fit $(0,\ldots, m_t\text{-}1)$ if t is the trait of measure and otherwise 0. The variance of the data vector was modeled as:

$$\text{Var}(\mathbf{y}) = \mathbf{Z} \, \text{Var}(\mathbf{u}) \, \mathbf{Z}' + \mathbf{W} \, \text{Var}(\mathbf{p}) \, \mathbf{W}' + \text{Var}(\mathbf{e}) \qquad [2]$$

where: $\text{Var}(\mathbf{u}) = \mathbf{A} \otimes \mathbf{G}$, with $\mathbf{A}$ = the additive genetic relationship matrix, $\otimes$ = Kronecker product function, and $\mathbf{G} = \begin{bmatrix} \mathbf{G}_{11} & \cdots & \mathbf{G}_{1t} \\ \vdots & \ddots & \vdots \\ \mathbf{G}_{t1} & \cdots & \mathbf{G}_{tt} \end{bmatrix}$ with $\mathbf{G}_{tt'} = \text{cov}(\mathbf{k}_{(m_t)}, \mathbf{k}_{(m_{t'})})$ = additive genetic covariance matrix of the genetic random regression coefficients for traits t and t′. Similarly, $\text{Var}(\mathbf{p}) = \mathbf{I} \otimes \mathbf{P}$, with $\mathbf{I}$ = identity matrix, and $\mathbf{P}_{tt'} = \text{cov}(\mathbf{l}_{(m_t)}, \mathbf{l}_{(m_{t'})})$ = covariance matrix that describes the permanent environmental component of an animals lactation within and between traits, which will be referred as the environmental effect further on in the paper. $\text{Var}(\mathbf{e}) = \mathbf{I} \otimes \mathbf{R}$, with $\mathbf{R}$ = diagonal matrix measurement error or residual variances ($\sigma_{e_t}^2$), assumed constant over DIM within trait and variable but independent between traits.

Stepwise-reduced Rank

In the multiple-trait lactation RR TDM with three parities and LEG(4) for both the genetic and environmental component; 3×5 random regression coefficients have to be estimated for both the genetic and environmental effects (i.e., 30 effects per animal in total). This corresponds with the estimation of 240 different (co)variances from over 1,3 million mixed model equations. For parameter estimation such a huge set of equations is not very

parsimonious and computationally too demanding with standard procedures. Therefore, the number of equations was reduced considerably by stepwise reducing the number of coefficients per animal. Without applying a complete canonical transformation, the regression coefficient were re-parameterized (as suggested by Misztal et al. (2000)) based on the eigenvectors ($\mathbf{V}$) and eigenvalues ($\mathbf{D}$) of the estimated CF coefficients, by setting the lowest eigenvalues (d_i of $\mathbf{D}$) equal to zero. In the first step (trait 1), the animal's regression coefficients for the first parity lactation (i.e., $\mathbf{k}_{(m_1)}$ and $\mathbf{l}_{(m_1)}$) were re-parameterized with the eigenvectors pertaining to the nonzero eigenvalues; creating a reduced rank CF (Eq. 3 and 4).

$$\mathbf{G} = \mathbf{V}_u\,\mathbf{D}_u\,\mathbf{V}_u' \qquad \text{and} \qquad \mathbf{P} = \mathbf{V}_p\,\mathbf{D}_p\,\mathbf{V}_p' \qquad [3]$$

$$\mathbf{k}^*_{(m_{t_r})} = \mathbf{V}_u^{'(r)}\,\mathbf{k}_{(m_1)} \qquad \text{and} \qquad \mathbf{l}^*_{(m_{t_r})} = \mathbf{V}_p^{'(r)}\,\mathbf{l}_{(m_1)} \qquad [4]$$

where $\mathbf{V}_u$ and $\mathbf{V}_p$ are matrices with eigenvectors as columns, and $\mathbf{D}_u$ and $\mathbf{D}_p$ are diagonal matrices with eigenvalues of the genetic and environmental CF-matrices respectively. $\mathbf{V}_x^{'(r)} = (m_{t_r} \times m_t)$ matrix containing only those eigenvectors of $\mathbf{V}_x$ that correspond to the r-largest, nonzero eigenvalues in $\mathbf{D}_x$, with x = u or p, m_{t_r} = reduced order of fit (i.e., number of r-largest eigenvalues), and m_t = original order of fit for trait(s) t. $\mathbf{k}^*_{(m_{t_r})}$ and $\mathbf{l}^*_{(m_{t_r})}$ are the re-parameterized set of coefficients for an animal of reduced size m_{t_r}, and can be different for the genetic and environmental component.

The procedure was applied according the following general steps. In step 1, CF coefficients ($\mathbf{G}$ and $\mathbf{P}$) are estimated for the first lactation only and, after that, re-parameterized to reduce the rank of the CF (Eq. [4]) as much as possible. In step 2, m-random regression coefficients of the second parity lactation ($\mathbf{k}_{(m_{t'})}$), or as many as acceptable, are included in the reduced set of coefficients ($\mathbf{k}^*_{(m_{t_r})}$). The new sets of coefficients in step s are therefore $\mathbf{k}^s_{(m_{t_r+t'})} = \left| \mathbf{k}^*_{(m_{t_r})}{}' \; \mathbf{k}_{(m_{t'})}{}' \right|'$ for the genetic, and $\mathbf{l}^s_{(m_{t_r+t'})} = \left| \mathbf{l}^*_{(m_{t_r})}{}' \; \mathbf{l}_{(m_{t'})}{}' \right|'$ for the environmental component. After re-estimation of $\mathbf{k}^s_{(m_{t_r+t'})}$ and $\mathbf{l}^s_{(m_{t_r+t'})}$, the procedure of stepwise-reducing can be repeated until all traits are included. Note that the new regression coefficients are defined for the new traits after re-parameterization, and no longer for the original traits. Further, multiplying the regression coefficients with the r-largest eigenvectors allows a reduction in the number of parameters but attempts to maintain the goodness of fit of the higher order LEG. All eigenvalues with a relative value of less than 2% were set equal to zero.

To illustrate the stepwise-reduced rank procedure two approaches were compared. Firstly, model INCL-x, in which information of all three parities was included stepwise;

starting with the first lactation and including coefficients of the later lactations in the subsequent steps to the new set of reduced rank coefficients. Secondly, model LACT-x, were first all CF parameters were estimated per parity, after that reduced and combined into a model that contained (reduced rank) lactation information of all three parities.

Table 1. Rank and reduced rank (in brackets) of the genetic and environmental covariance function matrices (G and P) for different steps in the approaches, INCL-x and LACT-x.

Model [1,2]		Order of fit (reduced rank) [3]			
Step	Name	**G**		**P**	
Step 1:	INCL-1	5	(3)	5	(4)
Step 2:	INCL-2a	6	(4)	7	(6)
Step 3:	INCL-2b	6	(4)	8	(6)
Step 4:	INCL-3a	7	(4)	9	(8)
Step 5:	INCL-3b	6		10	
Step 1:	LACT-1	5	(3)	5	(4)
Step 2:	LACT-2	5	(3)	5	(4)
Step 3:	LACT-3	5	(3)	5	(4)
Step 4:	LACT-MT	9		12	

[1] Information in approach INCL-x was included in five steps. Step 1 (INCL-1): single trait fourth order Legendre polynomial (LEG) model for first lactations only. Step 2 (INCL-2a): model with reduced rank covariance functions (CF) from INCL-1 and first three LEG coefficients for second lactations included. Step 3 (INCL-2b): model with reduced rank CF from INCL-2a and the 4-th and 5-th LEG coefficients for second lactations included. Step 4 (INCL-3a): model with reduced rank CF from INCL-2b and first three LEG coefficients for third lactations included. Step 5 (INCL-3b): model with reduced rank CF from INCL-3a and the 4-th and 5-th LEG coefficients for third lactations included.

[2] Information in approach LACT-x was included in 4 steps. Step 1 (LACT-1), step 2 (LACT-2), and step 3 (LACT-3): single trait analysis with a fourth order LEG model for respectively first, second, and third lactations separately. Step 4 (LACT-MT): model with reduced rank CF from LACT-1, LACT-2, and LACT-3 added together. Note that LACT-1 and INCL-1 are the same analysis.

[3] Reduced rank is the order of fit minus the number of eigenvalues with a relative value of less than 2%.

In step 1 of the first approach, INCL-x, the CF parameters for the first parity lactations (referred as INCL-1) were taken from Pool et al. (2000) [i.e., LEG(4) for both **G** and **P**]. In step 2 and 3 (INCL-2a and INCL-2b, respectively), lactation information of the second parity

was included. In step 2, the rank of the genetic and environmental CF-matrices in INCL-1 was reduced from 5 to 3 and 5 to 4, respectively (Table 1), and subsequently lactation information of the second parity was added by including the first three LEG coefficients. The new genetic and environmental CF-matrices in INCL-2a were of order six (3+3) and seven (4+3), respectively. In step 3 (i.e., INCL-2b) the rank of CF-matrices from INCL-2a was reduced with 2 and 1order, respectively (Table 1). Subsequently, the 4-th and 5-th LEG coefficients for the second parity were included. Lactation information of the third parity was included likewise in steps 4 and 5 (INCL-3a and INCL-3b, respectively). In the final step, INCL-3b, the genetic and environmental CF-matrices were fitted with order 6 and 10, respectively.

In the second approach, LACT-x, CF-matrices were estimated single trait for all three parities separately (i.e., step 1-3: LACT-1, LACT-2 and LACT-3), and LEG(4) for both the genetic and environmental effects. The CF-matrices of all three steps were reduced with two orders for the genetic, and one order for the environmental component to rank 3 and 4, respectively (Table 1). In step 4 (i.e., LACT-MT), the reduced rank CF-matrices of LACT-1, LACT-2, and LACT-3 were combined into a model with nine (3×3) coefficients per animal for the genetic component and 12 (3×4) for the environmental component.

Parameter Estimation

The high dimensionality of the model and the requirement of a relative large data (Pool et al., 2000) set brought about that the memory expensive deterministic variance component estimation programs were not suitable. Instead, Bayesian inference using Gibbs samples (Gelfand and Smith, 1990; Geman and Geman, 1984; Smith and Roberts, 1993) was used. The conditional distribution of the data was assumed multivariate normal:

$$\mathbf{y}|\mathbf{b},\mathbf{u},\mathbf{p},\sigma_e^2 \sim N(\mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp}, \mathbf{I}\,\sigma_e^2) \qquad [5]$$

Iterative BLUP according to Gauss-Seidel was used for solving the mixed model equations [details in (Janss and de Jong, 1999)]. In each round, vectors $\mathbf{b}$, $\mathbf{u}$, and $\mathbf{p}$ were updated where $\mathbf{u}$ and $\mathbf{p}$ were block wise sampled per animal from a multivariate normal distribution. Next variance components were updated. The update of $\sigma_{e_t}^2$ was sampled, assuming an uniform prior distribution, from the full conditional posterior distribution:

$$\sigma_{e_t}^2 \mid \mathbf{b},\mathbf{u},\mathbf{p},\mathbf{y} \sim SSE_t / \chi_{v_t}^2 \qquad [6]$$

which is inverted Chi-square distributed with $SSE_t = \mathbf{e}_t'\mathbf{e}_t$ (where $\mathbf{e}_t$ is that part of $\mathbf{e}$ [which follows from Eq. 1] pertaining to trait t); $v_t = N_t - (m_t + 1)$ degrees of freedom for trait t.

For, both **G** and **P**, the full conditional posterior distributions were Inverted Wishart (IW) distributed with dimension m (order of fit). Uniform priors were assumed, therefore the full conditional posterior distributions for **G** and **P** are:

$$\textbf{G}|\textbf{u} \sim IW(\textbf{SSG}^{-1}, \nu) \qquad [7]$$
$$\textbf{P}|\textbf{p} \sim IW(\textbf{SSP}\text{-}1, \nu) \qquad [8]$$

with $\nu = N_\bullet - (m_\bullet + 1)$ degrees of freedom, and scaling parameters **SSG** and **SSP** ($N_\bullet$ = number of observations for all traits, and $m_\bullet$ = dimension of the CF for **G** or **P**, for more details see Pool et al., 2000). The marginal posterior means obtained in this procedure were used as estimates for the variance components. The Gibbs sampler was ran until the effective chain size ($\tilde{\psi}$) was at least 50 independent samples long for all variance components. For computing of $\tilde{\psi}$, time series analyses was used [see (Sorensen, 1997) for details]. Burn-in was determined graphically and given in Table 2, together with total chain length and effective chain size for the different steps.

RESULTS

Burn-in and chain length to reach 50 independent samples was high for all steps in INCL-x and LACT-x but seemed not to increase with the complexity of the model (Table 2). Based on 50 independent samples the standard error is 14% of the standard deviation, which

Table 2. Burn-in, total chain length, and effective chain size for different steps in approach, INCL-x and LACT-x.

Model [1]	Step	Number of chains	Burn-in	Length of all chains in total	Effective chain size (min-max)
INCL-1	1	2	14,000	499,106	71 - 437
INCL-2a	2	5	30,000	776,950	262 - >6,000
INCL-2b	3	4	20,000	623,349	70 - >3,000
INCL-3a	4	3	16,000	537,405	95 - >9,000
INCL-3b	5	5	10,000	551,562	79 - >15,000
LACT-1	1	2	14,000	499,106	71 - 437
LACT-2	2	2	20,000	556,137	82 - 473
LACT-3	3	2	16,000	652,385	89 - 521
LACT-MT	4	6	10,000	901,158	171 - >6,000

[1] for definition of names see notes in Table 1

Table 4. Eigenvalues and relative proportions (in brackets) for the genetic and environmental covariance function matrices for different steps in the approaches, INCL-x and LACT-x.

Steps[2] Order	First	Second	Third	Fourth	Fifth	Sixth	Seventh	Eighth	Ninth	Tenth	Eleventh	Twelfth	Sum[1]
Genetic eigenvalues (proportion)													
INCL-1	9.80 (87.0)	1.11 (9.8)	0.26 (2.3)	0.06 (0.5)	0.05 (0.4)								11.17 (99.0)
INCL-2a	24.05 (79.6)	4.05 (13.4)	1.02 (3.4)	0.75 (2.5)	0.30 (1.0)	0.04 (0.1)							29.87 (98.9)
INCL-2b	26.47 (77.6)	5.27 (15.4)	1.26 (3.7)	0.97 (2.8)	0.11 (0.4)	0.03 (0.1)							33.97 (99.6)
INCL-3a	39.39 (71.5)	10.48 (19.0)	2.98 (5.4)	1.49 (2.7)	0.40 (0.7)	0.30 (0.6)	0.08 (0.1)						54.34 (98.6)
INCL-3b	38.75 (68.4)	11.99 (21.1)	4.12 (7.3)	1.60 (2.8)	0.16 (0.3)	0.06 (0.1)							56.46 (99.6)
LACT-1	9.80 (87.0)	1.11 (9.8)	0.26 (2.3)	0.06 (0.5)	0.05 (0.4)								11.17 (99.0)
LACT-2	12.44 (76.4)	3.26 (20.0)	0.43 (2.6)	0.13 (0.8)	0.03 (0.2)								16.13 (99.0)
LACT-3	9.95 (67.8)	4.11 (28.0)	0.39 (2.6)	0.18 (1.2)	0.06 (0.4)								14.45 (98.4)
LACT-MT	33.32 (70.5)	9.31 (19.7)	1.97 (4.2)	1.52 (3.2)	0.53 (1.1)	0.34 (0.7)	0.12 (0.3)	0.10 (0.2)	0.05 (0.1)				46.12 (97.6)
Environmental eigenvalues (proportion)													
INCL-1	8.96 (73.4)	1.82 (14.9)	0.84 (6.8)	0.43 (3.5)	0.17 (1.4)								12.05 (98.6)
INCL-2a	16.00 (51.9)	6.34 (20.6)	3.97 (12.9)	1.66 (5.4)	1.56 (5.1)	0.84 (2.7)	0.46 (1.4)						30.37 (98.5)
INCL-2b	14.82 (49.4)	6.00 (20.0)	4.26 (14.2)	1.83 (6.1)	1.38 (4.6)	0.89 (3.0)	0.58 (1.9)	0.23 (0.8)					29.18 (97.3)
INCL-3a	23.86 (43.0)	9.32 (16.8)	6.95 (12.5)	3.93 (10.7)	3.35 (6.0)	2.64 (4.7)	1.34 (2.4)	1.30 (2.3)	0.89 (1.6)				54.69 (98.4)
INCL-3b	25.97 (43.0)	9.43 (15.6)	7.94 (13.2)	6.11 (10.1)	3.56 (5.9)	2.91 (4.8)	1.60 (2.7)	1.32 (2.2)	1.00 (1.7)	0.50 (0.8)			38.84 (97.5)
LACT-1	8.96 (73.4)	1.82 (14.9)	0.84 (6.8)	0.43 (3.5)	0.17 (1.4)								12.05 (98.6)
LACT-2	14.13 (67.9)	4.24 (20.4)	1.47 (7.0)	0.75 (3.6)	0.23 (1.1)								20.59 (98.9)
LACT-3	19.53 (67.5)	5.74 (19.8)	2.14 (7.4)	1.01 (3.5)	0.51 (1.8)								28.42 (98.2)
LACT-MT	27.06 (44.5)	9.23 (15.2)	6.50 (10.7)	5.72 (9.4)	3.56 (5.8)	2.60 (4.3)	1.66 (2.7)	1.37 (2.3)	1.10 (1.8)	0.82 (1.4)	0.71 (1.2)	0.42 (0.7)	57.70 (95.0)

1 Sum of eigenvalues with a proportion greater than 2% (i.e., the non-zero eigenvalues; in bold), and the relative amount of variance explained compared to the sum of all eigenvalues.

2 Note, that the steps INCL-1 and LACT-1 are the same analysis (for definitions of names see notes Table 1).

was assumed as reasonable. Residual variance estimates were lowest for first parity lactations and somewhat higher for second and third (Table 3). Including information stepwise in INCL-x resulted in somewhat higher residuals for first and second parity lactations (INCL-3b) compared to the single trait analyses (LACT-1 to 3). With all information included (the final steps INCL-3b and LACT-MT) residual variances from INCL-3b were respectively, 0.4 and 0.3 kg^2 higher for the first and second parity lactations, and 0.3 kg^2 lower for third ones. This suggests that lactation information from first and second parities was weighed incorrect in INCL-3b compared to the same information in LACT-MT. However, if only the first three LEG coefficients were included (INCL-2a and 3a) the residuals were higher as with a full fit (INCL-2b, INCL-3b, and LACT-x); showing that higher orders of fit were essential.

Table 3. Residual variances ($\sigma^2_{e_t}$, in squared kilograms) and posterior standard deviations (in brackets) of milk yield for first, second, and third parity lactations for different steps in the approaches, INCL-x and LACT-x.

Steps [1]	$\sigma^2_{e_t}$ (posterior standard deviations)		
	Lactation 1	Lactation 2	Lactation 3
INCL-1	2.46 (0.01)		
INCL-2a	2.55 (0.01)	4.48 (0.02)	
INCL-2b	2.76 (0.01)	3.68 (0.02)	
INCL-3a	2.76 (0.01)	3.97 (0.02)	5.63 (0.03)
INCL-3b	2.93 (0.01)	4.03 (0.02)	4.38 (0.03)
LACT-1	2.46 (0.01)		
LACT-2		3.62 (0.02)	
LACT-3			4.33 (0.03)
LACT-MT	2.55 (0.01)	3.79 (0.02)	4.66 (0.03)

[1] for definition of names see notes in Table 1

Scaling the CF-matrices by the r-largest eigenvectors ensured a correction for the goodness of fit of the higher order polynomials. In the first approach, INCL-x, lactation information was included partly step by step; a reduction of 9 orders for the genetic and 5 for the environmental component was achieved (i.e., a reduction of 0.7 million equations, which is more than half). In the second approach, LACT-x, parities were analyzed separately as single traits, the rank of CF-matrices was reduced and subsequently combined into one multiple-trait analysis; a reduction of 6 orders for the genetic and 3 for environmental component was achieved (i.e., a reduction of 0.5 million equations, which is still large but

Figure 1: Environmental variances of milk yield expected among DIM predicted for first, second, and third parities for different steps in the approaches, INCL-x and LACT-x (for definitions of names see notes Table 1).
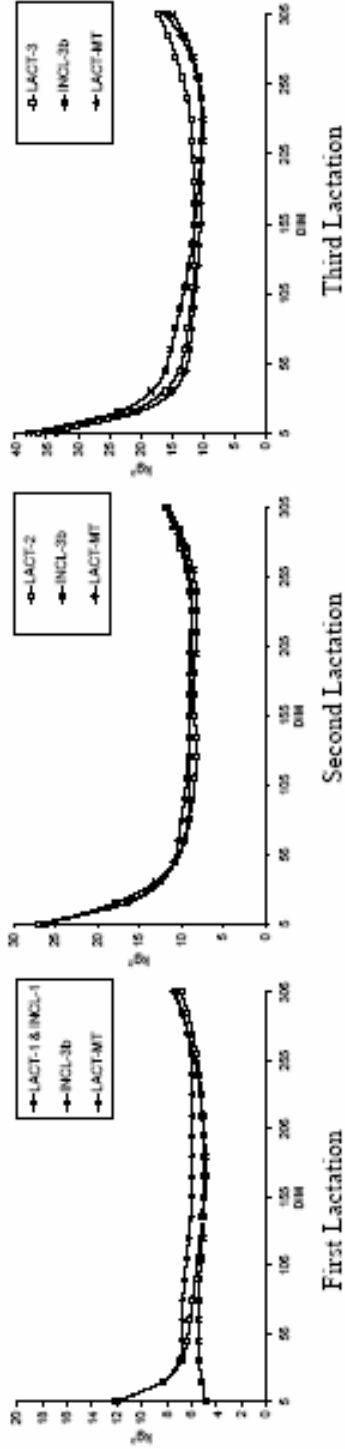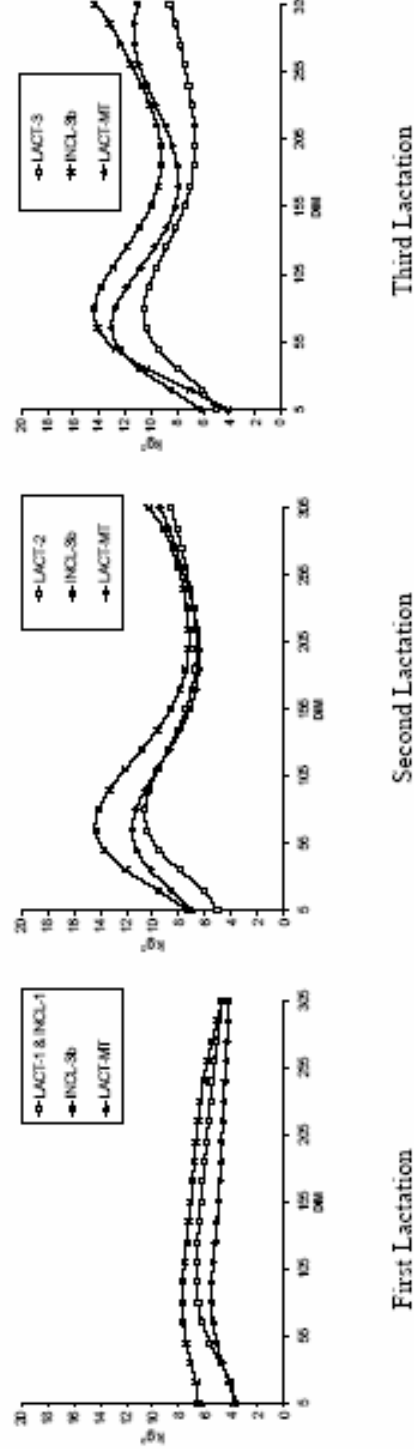
Figure 2: Genetic variances of milk yield expected among DIM predicted for first, second, and third parities for different steps in the approaches, LACT-x and INCL-x (for definitions of names see notes Table 1).

72

step was for INCL-3b respectively 4 and 9, and for LACT-MT respectively 5 and 10 (i.e., if the sum of all eigenvalues assumed zero was less than 2%). Therefore, in a final reduction step the overall reduction will be 15 (30-15) parameters per animal for LACT-x and 17 (30-13) for INCL-x (i.e., a reduction in number of equations of respectively 63 and 56%).

The importance of each order of fit was expressed by the corresponding eigenvalues as a relative proportion of the sum of all eigenvalues for each step (Table 4). Eigenvalues of the genetic component changed with the complexity of the model, actually the leading eigenvalue increased in value with the complexity, but it's relative importance decreased if more information was included (from INCL-1 to INCL-3b). The decrease in relative importance of the leading eigenvalue also occurred in the single trait analyses (LACT-1 to 3) and shows that higher orders are more important for fitting lactation curves from second and third parities. For the environmental component, the pattern in eigenvalues was similar, although the relative proportion of the smaller eigenvalues was larger. This means that the rank of the environmental CF-matrices could not be reduced as far as for the genetic ones (see also Table 1). By setting the eigenvalues with a relative proportion of less than 2% (Table 4, in bold) equal to zero, each reduced rank step accounted for at minimum 97.3% (INCL-2b) and at maximum 99.6% (INCL-2b) of the sum of all eigenvalues. In the final steps (INCL-3b and LACT-MT) the sum of all eigenvalues was, respectively, 56.68 and 47.26 for the genetic part, and 60.34 and 60.75 for the environmental component. Comparing those results shows that approach INCL-x did account for more genetic variation than LACT-x, despite a lower order of fit for INCL-3b (i.e., 6 and 10 for the genetic and environmental part, respectively, compared to 9 and 12 in LACT-MT). Because lactation information from later parities shows more variability, the higher sum of eigenvalues in INCL-3b might indicate that later parities are predicted more precise than in LACT-MT. However, based on the number of eigenvalues smaller than 2%, the reduced rank of the final CF-matrices of both approaches were equal (e.g., 4 and 8 for respectively the genetic and environmental component) and therefore comparable.

(Co)variance Functions Estimates

Genetic and environmental variances were calculated from the CF estimates among each DIM for each step in the reduced rank procedure. The curves of environmental variances were high at the beginning and end of lactation, lower in between, and its overall level increased with lactation number (Figure 1). The goodness of fit compared to the single trait analyses (LACT-1, 2, and 3) was best for second parity lactations. For first parities, only step INCL-3b showed a systematic lower start of the curve after that all information of third parities was included. This suggest that information included firstly (i.e., LEG coefficients of the first parity lactations) is not properly weighted anymore in INCL-3b (i.e., after four steps of
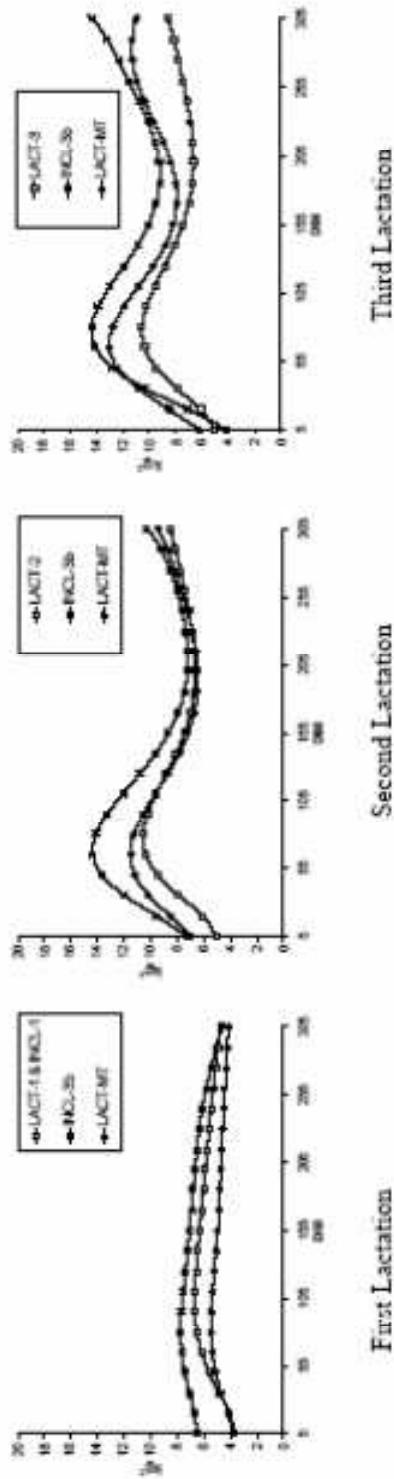
Figure 3: Heritability (h2) of milk yield expected among DIM predicted for first, second, and third parities for different steps in the approaches, LACT-x and INCL-x (for definitions of names see notes Table 1).
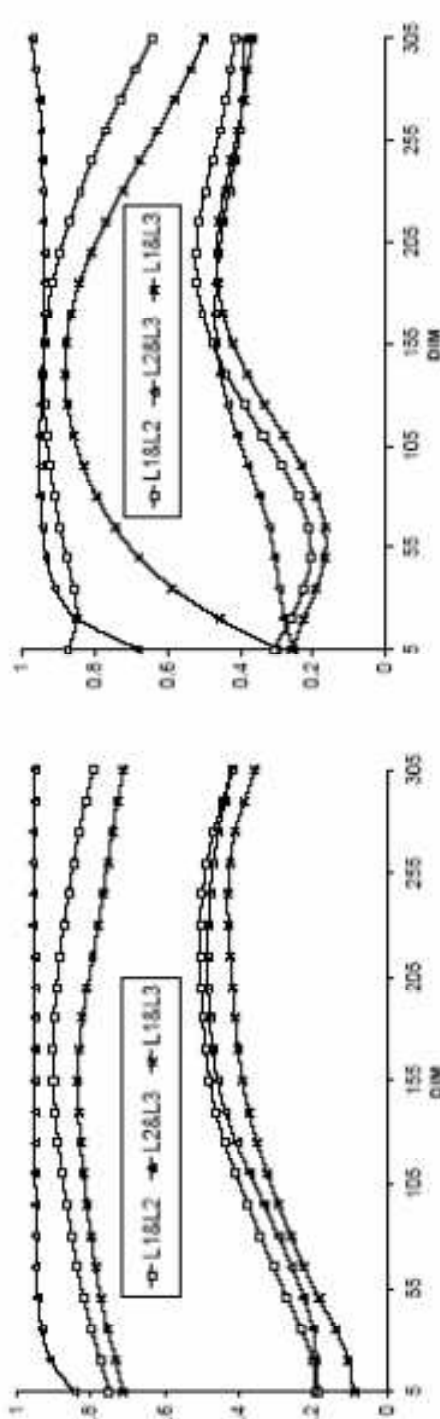

Figure 4: Predictions of genetic (above Legend) and environmental correlations (below Legend) expected among DIM between first (L1), second (L2), and third (L3) lactations from steps, LACT-MT (on the left) and INCL-3b (on the right).

74

information inclusion). Curves of predictions for genetic variances (Figure 2) varied between different steps more than for the environmental ones. The genetic curve tended to increase at peak yield (observed around day 65) and towards the end of the trajectory for the second and even more for the third parities, which was also observed for the single trait analyses. Overall, the single trait analyses (LACT-1 to 3) seemed to be fitted better by LACT-MT than INCL-3b. For heritability estimates (Figure 3) the curves showed similar shapes for all model steps, lower at the beginning and end of the lactation period, and up to 0.46 around day 100. Overall, heritability curves were as expected and not really different for the higher order, (i.e., more) complex model steps. However, the heritability curve for first parities was structural higher at the beginning for INCL-3b and lower in the middle part for LACT-MT compared to the single trait analysis (LACT-1 & INCL-1). For second parities, differences were relatively small with a tendency of slightly lower values for single trait analysis. For third parities the same pattern as for second parities was observed, but differences observed were larger.

To indicate the relationship between parities, the genetic and environmental correlation estimates between first, second, and third parities from the model steps INCL-3b and LACT-MT (i.e., if al lactation information of all three parities was included) were presented in Figure 4. In general the genetic correlations were high between all three lactations, however, although the correlation from LACT-MT hardly changed with DIM, those for INCL-3b varied considerable more and seemed less realistic. As expected, the correlation between lactation information from first and third parities was high, but lower than for first and second, and second and third parities in both models. Also the correlation between lactation information from first and second parities was lower than those between second and third parities, except at the beginning of the lactation curve in model step INCL-3b. Environmental correlations varied from 0.1 to 0.5 for both models, starting low for days early in lactation and increasing towards the end of lactation with a peak 0.5 around day 205.

DISCUSSION

Model choices and data selections were based on result from previous work (Pool and Meuwissen, 1999; 2000; Pool et al., 2000). Concerning the choice of the function to describe the lactation curve it was found that higher order functions were necessary for a sufficiently accurate fit (Guo and Swalve, 1997a; Pool and Meuwissen, 1999). Based on the goodness of fit and mean square errors of predictions a fourth order LEG function was found to be sufficient (Pool and Meuwissen, 2000). Further, to obtain consistent parameter estimates, a large data set (Pool et al., 2000) with only complete lactation records (Pool and Meuwissen, 2000) was suggested. By analyzing only complete lactations, any implicit extrapolation was avoided but might have introduced some selection bias. However, the selection bias had less effect on the estimates of the parameters than extrapolations of the incomplete lactations (Pool and Meuwissen, 2000). The need of a large data set made the number of equations that need

to be solved large. With a full multiple-trait RR TDM for three parities, a fourth order LEG (i.e., CF-matrices of dimension 15), and data from 23,700 animals (63,583 entries in the pedigree), over 1.3 million equations had to be solved. Such a large model is hard to solve and not very parsimonious, therefore a drastically reduction of the number of parameters would be needful. This problem becomes even larger when we would estimate the CF parameters for milk, fat, and protein over their lactations simultaneously, but can be solved by the procedure investigated in this paper.

As an alternative for the multiple-trait TDM, Wiggans and Goddard (1997) suggested a canonical transformation analyzing only the largest canonical variates as univariate analyses. Meyer (1997) showed that the canonical decomposition could be applied easily to multiple trait CF models, assuming equal design matrices. Van der Werf et al. (1998) extended the algorithm with missing data to an infinite number of traits. The genetic and environmental covariance matrices (**G** and **P**) were decomposed simultaneously, and by setting the lowest eigenvalues equal to zero the rank of the CF-matrices was reduced. With the eigenvalue decomposition procedure described here, the ranks of **G** and **P** were reduced separately and has the advantage that: 1) **G** could be modeled with lower rank than **P**. The lower rank for **G** was achieved by separate transformation whereas the number of parameters with a canonical transformation will be equal to the rank of the **P** (i.e., the CF-matrix with the largest rank); 2) the least variable effects obtain less weights when transformed by the corresponding eigenvectors whereas with canonical transformation the least heritable effects are eliminated, but, actually the least heritable effect could affect the environmental variances significantly; 3) the canonical transformation is limited to decomposing the matrices of two random effects simultaneously whereas separate transformation can be performed independently on many random effects. Note that the second advantage implies that the traits analyzed should have (approximately) the same phenotypic variances [i.e., should be scaled to some (arbitrary) value]; if not the eigenvalues of the less variable traits will be eliminated first. Here in this study, the phenotypic variances were approximately on the same level, because all three traits were milk yields.

Because the single trait analyses of later lactations (LACT-2 and 3) cannot account for selection, estimates are biased. This caused the slightly lower genetic variance and heritability estimates and possibly also the lower sum of genetic eigenvalues in LACT-MT. However, the residual variances from LACT-MT were lower (except for third parities) and indicated a better fit of the data. Further the smaller number of records for third parities compared to first and second possibly resulted in a better fit of the first two lactations at the expense of the third. Except a slightly lower genetic variance curve for first parity lactations, it seemed that LACT-MT had a more appropriate fit, and gave more realistic heritability curves.

By setting the eigenvalues with a relative value of less than 2% equal to zero, the rank of the CF-matrices was evenly reduced in each step; two orders for the genetic CF-matrix (except INCL-3a) and one for the environmental one (except INCL-2b) (Table 1). Two orders less, means three non-zero eigenvalues for the additive genetic CF-matrix which was also suggested by Olori et al. (1999). Re-running of step INCL-2b, while assuming only one eigenvalue zero instead of two, indicated that the increased peak observed for the genetic variance in second parities (as observed for INCL-3b, Figure 2) would decrease, but not completely disappear (results not shown). Actually, the rank reduction of the environmental CF-matrix in INCL-x was not 5 orders but only 4. Re-running of INCL-3a with two genetic eigenvalues assumed zero instead of three did not gave any changes. Further, in each step the sum of eigenvalues assumed zero was always less than 2% (i.e., over 98% of the variation was accounted for), except for INCL-2b, which was 2.7%. Therefore, it seems that for a good fit, the sum of eigenvalues set to zero should be less than 2% in any step.

Although the number of parameters could be halved, the memory requirements of deterministic variance component estimation programs based on direct solving the mixed model equations were still very large. Therefore, Gibbs sampling was used for parameter estimation, and memory requirements reduced to less than 50-MB of RAM for the largest model (LACT-MT). As a consequence, parameter estimation was possible with limited computing requirements and within a reasonable period of time.

Within parity both approaches, INCL-x and LACT-x, showed good fits of variance curves, although the starting of the genetic curve for first parity lactations in INCL-3b was different and seems to be the result of unequal weighting which was less but still present in LACT-MT. The irregular pattern observed in second but especially for third parities might be improved by: 1) a more evenly distribution of records over parities by including more informative data of more animals or by combining second and third parities together; 2) a correction for heterogeneous variances among DIM for the residuals (Jamrozik et al., 1997c; Olori et al., 1999) and/or for the random effects (Pool and Meuwissen, 2000).

Compared to literature, estimated variance components along DIM were in general on the same level, although differences were considerable between studies (Jamrozik et al., 1997c; Mäntisaari, 1999; Olori et al., 1999; Rekaya et al., 1999; Van der Werf et al., 1998). The shape predicted for the genetic curve was lower at the beginning and end of lactation, and higher around peak where other studies found higher values for the ends of the trajectory. Further, heritability estimates were slightly lower at the edges of the curve and higher in-between compared to estimates by Jamrozik et al (1997c), and in general higher compared to those reported by Mäntysaari (1999). Compared to 305-d lactation yields, heritabilities of individual test-day yields are often lower because of accounting for correlations among test days

Table 5. Heritability estimates, genetic and environmental correlations among 305-d lactation milk yield for first (L1), second (L2), and third (L3) parity lactations for different steps in the approaches, INCL-x and LACT-x.

	Heritability			Genetic (environmental) correlations		
Steps [1]	L1	L2	L3	L1&L2	L2&L3	L1&L3
INCL-1	0.52					
INCL-2b	0.59	0.56		0.92 (0.35)		
INCL-3b	0.53	0.50	0.48	0.92 (0.44)	0.97 (0.42)	0.82 (0.39)
LACT-1	0.52					
LACT-2		0.47				
LACT-3			0.35			
LACT-MT	0.43	0.47	0.48	0.90 (0.49)	0.95 (0.44)	0.81 (0.41)

[1] For definition of names see notes in Table 1

305-d yield heritability estimates for the single trait analyses (LACT-1 to 3, Table 5) decreased with lactation number, as expected, due to selection bias over parities. Because daily heritability estimates in this study were high, 305-d yield heritabilities were even higher. However, values for first parity lactation were similar to Janss and De Jong (1999). Genetic correlations between lactations from parity 1 and 2 were higher than those between 2 and 3, while the correlations between 1 and 3 were lowest, as expected from literature (Rekaya et al., 1999).

Overall the reduction of number of parameters with approach LACT-x seemed to yield a more realistic fit. This approach allowed halving the number of parameters to be estimated per animal without reducing the goodness of fit considerably. However, the sum of eigenvalues assumed zero should not be larger than 2% of the sum of all eigenvalues. Compared to a full multiple-trait TDM, the stepwise-reduced rank procedure is more parsimonious and needs considerable less computational requirements, especially, if applied in large-scale genetic evaluations. For a further extension to a multi lactation and multiple-trait RR TDM for milk, fat, and protein the approach LACT-x is recommended. Actually, first reducing the rank within the traits milk, fat, and protein, and then analyze milk, fat, and protein simultaneously over traits, and after which a further, final step of reduction in the number of parameters can be applied.

Comparison of breeding values predicted with a repeatability and a fourth order random regression test-day model.

(M. H. Pool[a] and T.H.E. Meuwissen[b])

[a]   Wageningen Institute of Animal Science (WIAS).
[b]   Department of Genetics and Reproduction. Institute of Animal Health and Science
(ID-Lelystad) P.O. Box 65, 8200 AB Lelystad, The Netherlands

INTRODUCTION

Breeding values (**EBVs**) of dairy cows currently predicted in the Netherlands are from an animal lactation model based on information of realized or projected 305-d lactation yield (Wilmink 1987b). Today, the use of single test-day records instead of 305-d lactation yield is of more interest for the genetic evaluation of dairy cows as well as a tool for farm-management, because it provides additional information about the progression of milk production during the lactation period. The first countries that have implemented a national evaluation model for dairy cattle based on individual test-day records [i.e., a test-day model (**TDM**)] by using random regression techniques are Canada in 1999 (Schaeffer et al., 2000) and Finland in 2000 (Lidauer et al., 2000). In Germany the lactation model has been replaced already 1996 by a multi-trait lactation repeatability TDM (Reents and Dopp, 1996), assuming each test-day as a repeated measurement.

The advantage of a TDM compared to a lactation model is that the former can correct more precise for effects as herd-test-dates (Swalve, 1995) simultaneously with the prediction of breeding values. Above that, if test-days are not interpreted as correlated traits with correlations less than one, and not as measures of a repeated trait, a TDM includes information about the progression of the production during lactation in the model. EBVs are provided for each day along the trajectory and therefore the TDM can describe differences in the shape of lactation curves between animals (Schaeffer and Dekkers, 1994). In this study, the random regression (**RR**) approach described by Schaeffer and Dekkers (1994) was applied. In the RR-TDM the lactation curve is modeled by a random function for each animal and the underlying covariance function structure is estimate directly from the data (Meyer, 1998). A RR-TDM provide thus information about both the level and shape (i.e. progression of production) of the lactation curve, where a lactation model fits only the level. In stead of a lactation model, a repeatability test-day model (**RPM**) was used in this study to mimic the current situation. In the RPM genetic variation is assumed constant during over the whole lactation period, which

means that the EBV of 305-d yield or for any part of the lactation period is just the average genetic daily prediction times the length of the (part)lactation. With the RR-TDM, the genetic merit of an animal is different for each DIM along the lactation trajectory and therefore the features of a RR-TDM are not fully expressed if EBVs are summarized into 305-d productions. Therefore it is better to express the EBVs from a RR-TDM as genetic merit lactation curves (Swalve, 2000) or by parameters that describe the persistency of a lactation to supply all information about the genetic value of milk yield. The RR-TDM of today are not only a desired tool but are for genetic reasons valuable in order to reduce the generation interval and to provide a more accurate prediction of genetic merit (Swalve, 2000). In this study, EBVs were predicted with a TDM using single test-day records and compared to a RPM. We compared the TDM with a RPM instead of a lactation model because results from a RPM would be better comparable to a TDM, (i.e., comparable models and similar fixed effect corrections). However, the RPM models only the level of production as the lactation model does and therefore it was assumed that selection for milk production with both models was for the same trait, i.e. same type of lactation curve.

MATERIALS AND METHODS

Data

First lactation test-day records from Holstein Friesian dairy cows calved in the period April 1990 until January 1999 from the northern part of the Netherlands were used. Selection criteria for the first lactation records were: known date of birth of heifer (i.e. for pedigree information), at least 50% Holstein-Friesian, age at calving 22 to 32 months old, all test-day records realized on the same farm, and from herds with at least 25 first lactations in the data set. After selection over 1.45 million first lactations of more than 10,000 herds were available. For the current analyses only lactation records of herds in the north (identified by zip code) were used and reduced the data set to 282,548 first lactations with in total 2,563,919 test-day records. Animals with records were offspring of 8,323 sires and 197,226 dams and pedigree data contained in total 577,769 entries (24,583 sires and 553,186 cows).

Model

Test-day records were modeled by a RPM, as Legendre polynomials (LEG) (Kirkpatrick et al., 1990; 1994) with a 0-th order of fit [LEG(0)], and by a TDM with a 4-th order Legendre polynomial [LEG(4)]. Model parameters were estimated by Pool et al. (2000). For LEG(0) one order was fitted for both the genetic and permanent environmental part (i.e., 2 RR coefficients per animal), and five orders of fit for LEG(4) (i.e.,10 RR coefficients per cow, five for the genetic and five for the permanent environmental component). Thus the RPM model was modeled as a RR-TDM with only one order of fit and was assumed to mimic a

lactation model. The RPM did thus correct for the effect of herd-test-date, which is differs from the currently lactation model used in the Netherlands. However, the prediction of average daily milk yield multiplied by 305 is comparable to a 305-d production.

The general model of analyses was:

$$y_{ij} = \mathbf{x}_{ij}'\boldsymbol{\beta} + \boldsymbol{\phi}_{ij(m)}'\mathbf{k}_{i(m)} + \boldsymbol{\phi}_{ij(m)}'\mathbf{l}_{i(m)} + e_{ij} \qquad [1]$$

where, y_{ij} = test-day milk yield j for animal i; $\mathbf{x}_{ij}'$ = incidence row vector for fixed effects $\boldsymbol{\beta}$; $\boldsymbol{\beta}$ = [μ; ys; age; cDIM; HTD]', where μ = the overall mean, ys = year season of calving (classes of 3 months within year), age = age at calving (age classes of 4 months), cDIM = weekly classes for days in milk and modeled the shape of the average lactation curve (44 classes), and HTD = herd-test date effect (181,716 classes); $\boldsymbol{\phi}_{ij(m)}'$ = $\mathbf{t}_{ij}\boldsymbol{\Lambda}_m$ = incidence row vector for the RR coefficients of test-day record j for animal i, with $\mathbf{t}_{ij}$ = (1 by m) row vector with standardized days in milk (ranging from –1 to 1) to the power equal to the order of fit [0...(m-1)], with m = the order of fit, and $\boldsymbol{\Lambda}_m$ = a matrix of polynomial coefficients on the Legendre scale (3); $\mathbf{k}_{i(m)}$ and $\mathbf{l}_{i(m)}$ are (m by 1) vectors of covariance function coefficients for animal i for respectively the additive genetic and permanent environmental effect; e_{ij} = residual term of test-day record j for animal i and was assumed to model measurement errors. The genetic (co)variance function assumed by the model was: Var(**u**) = **A** ⊗ **G**, where **A** = additive genetic relationship matrix, ⊗ = Kronecker product function, and **G** = var($\mathbf{k}_{(m)}$) = additive genetic covariance matrix of the genetic RR coefficients. Similarly for permanent environment: Var(**p**) = **I** ⊗ **P**, where **I** = identity matrix, and **P** = var($\mathbf{l}_{(m)}$) = permanent environmental covariance matrix of the RR coefficients. The residual variance structure (σ_e^2) was assumed diagonal and constant over days in milk (**DIM**).

Model Comparison

EBVs were estimated for a series of times twice per year (in June and December). Starting in 1991 with one year of test-day data, up to 1999 with nine years of test-day data, a series of sub data sets was created by deleting all test-day records after a certain date. EBVs were estimated in June and December from each year, except in the year 1991 where only the December run was performed.

Average EBVs were groups of animals were compared for cows and sires. Young bulls were grouped by year of birth and compared for different EBVs in a row based on different amounts of information (i.e. running and complete lactation records for first versus second crop daughters). All EBVs were compared to the average EBV of all cows born in the year 1989 (i.e., the first group of cows with all test-day records available for complete lactations).

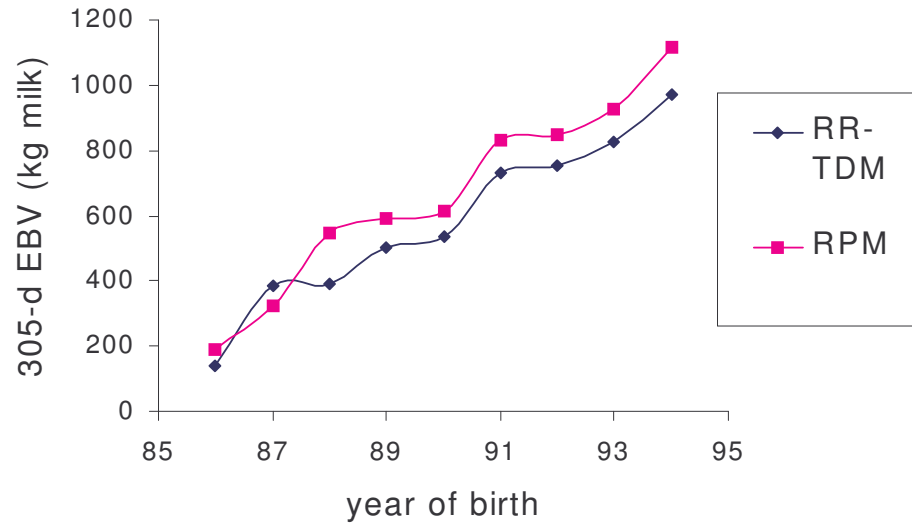Figure 1:   Trend in 305-d EBVs for youngbulls from a random regression test-day model (RR-TDM) and a repeatability test-day model (RPM). Youngbulls are grouped by year of birth and EBVs are standardized to cows born in the year 1989.
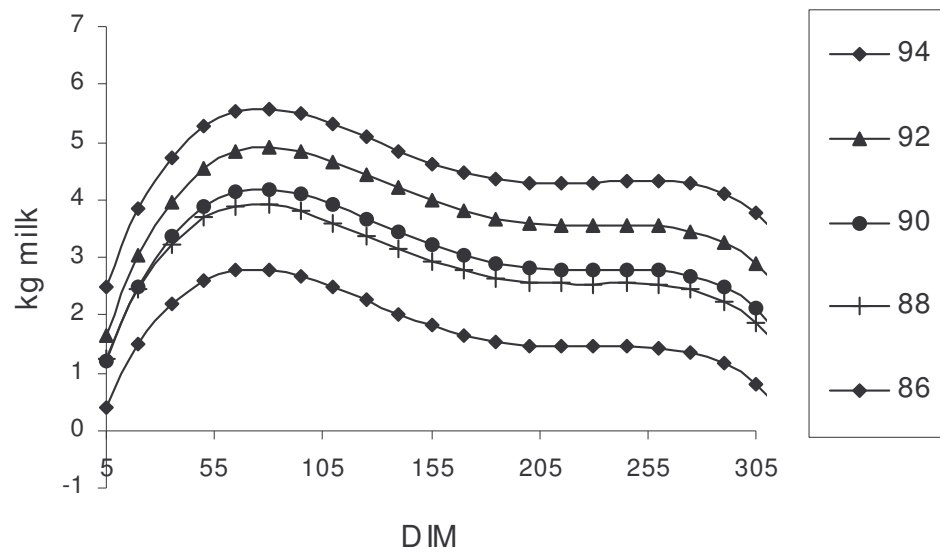

Figure 2:   Genetic merit lactation curves for groups of progeny tested bulls (grouped by birth year) from a random regression test-day model. EBVs shown were from the December 1999 run

RESULT AND DISCUSSION

Correlations between 305-d EBVs from the RPM and the RR-TDM where in general high. For young bulls (grouped by year of birth) correlations between 305-d EBVs, ranged from 0.85 to 0.99 when compared for pedigree and second crop daughter information, respectively. Liu et al. (1998) presented lower correlations and compared to correlations presented for a multi-trait RR-TDM by Schaeffer et al. (2000) values in this study were slightly higher. Standard deviations for 305-d EBVs were in the RR-TDM as high as for the RPM, indicating that the RR-TDM would model somewhat more variability between the animals.

In the December 1999 run, the trend in 305-d EBVs for young bulls (Figure 1) was 106 kg of milk per year for the RPM and 94 kg of milk per year for from the RR-TDM. The trend for the shape of the genetic lactation curve was shown in Figure 2. Based on the RR-TDM the shape was similar for different groups of young bulls, indicating that selection in the past had been for a general increase of the level of production, and not for more or less persistent animals. The average level of 305-d EBVs in the RR-TDM was lower than in the RPM and is possibly the affected by differences in fixed effect corrections or the result possible selection bias in the data. Further, it seems that the RR-TDM versus RPM expresses more differences between animals when the amount of information is small (first sub sets, 1991). Also the increase of EBVs over years was higher in the RR-TDM. However, comparisons presented so far in this study were based on a 305-d lactation yield, which do not include all information provided by the RR-TDM.

Actually, as presented in Figure 3, the EBVs from the RR-TDM should be expressed as curves with the value of genetic merit over the whole lactation trajectory. Curves with genetic merit from the RPM (dotted lines) are flat and express only the average level of production. Conversely, the genetic merit lactation curves of the RR-TDM show a variable additive genetic daily EBV across DIM (i.e. as a deviation from the average lactation curve). Lactation curves for different groups of animal were similar in shape and seemed to vary more in level of production than for progression of production. However, in Figure 4 it is shown that the curves of individual animals do actually differences for both the level and progression of production. For example, the daily EBVs of sire 7 increased continuously with DIM, where sire 5 only showed a decline. Based on the RPM (the two dotted lines in Figure 4) difference in EBV for sires 4 and 6 was small (0.6 kg difference a day) were the RR-TDM shows a more persistent genetic merit lactation curve for sire 6 compared to sire 4. Based on the 305-d EBV, the value for sire 4 was equal in both models were the value for sire 6 was for the RR-TDM 90 kg lower than for the RPM and indicates an over prediction of the 305-d EBV of sire 4 in the RPM.
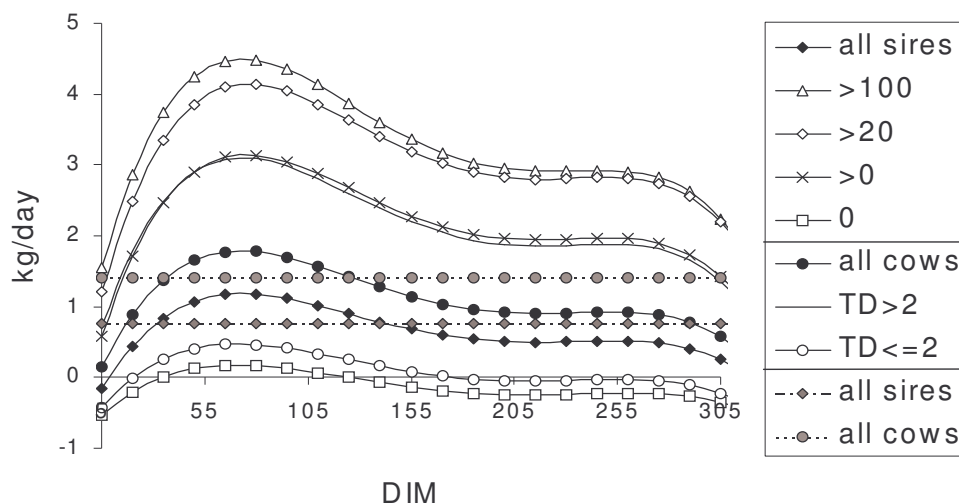
Figure 3:   Genetic merit lactation curves for different groups of animals from a random regression test-day model (solid lines) and a repeatability test-day model (dotted lines). EBVs shown were from the December 1999 run (i.e. the complete data set with 2.56 million test-day records from 282,548 first lactations).

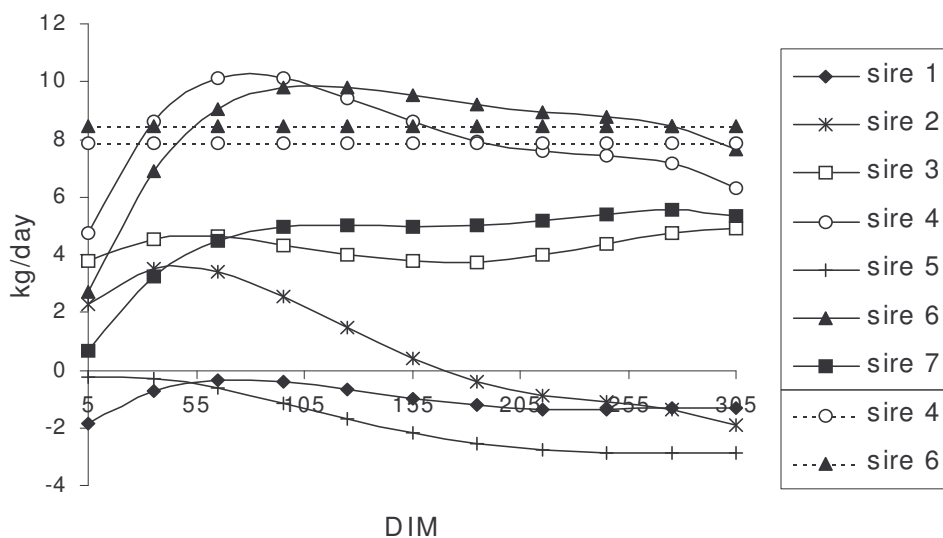

Figure 4   Genetic merit lactation curves for seven different individual sires from a random regression test-day model (solid lines) and for two sires also from a repeatability test-day model (dotted lines). EBVs shown were from the December 1999 run for sires born in 1992.

In Table 1 values are calculated as a measure for the stability of EBVs to express difference between EBV of young bulls when they are on average 4.5 and 6 years old (i.e., EBVs based on information of running and complete lactations from first crop daughters, respectively). EBVs of young bulls (grouped by birth year) predicted by the RPM were at the age of 4.5 years in general lower than at the age of 6 years old, where the RR-TDM showed slightly lower EBVs at the age of 6 years old. However, differences were relatively small. To

Table 1: Average difference in breeding values predicted (EBV) for groups of youngbulls (by birth year) calculated as EBV(running lactations) minus EBV(complete lactations) (i.e., EBVs were based on first crop daughters when the average age of youngbulls was, respectively, 4.5 years and 6 years old) by the repeatability test-day model (RPM) and the random regression test-day model (RR-TDM)

Birth-year	overall		more persistent		less persistent	
	RPM	RR-TDM	RPM	RR-TDM	RPM	RR-TDM
1993	-19.1	37.1	-76.7	14.6	47.5	63.0
1992	-36.6	3.8	-111.7	-15.9	41.8	24.2
1991	-53.9	19.1	-86.7	5.0	-20.6	33.4
1990	-31.7	4.0	-67.9	-9.3	2.5	16.6
1989	27.2	21.7	34.9	48.0	17.8	-7.6
1988	-28.76	1.95	-100.9	-40.9	46.7	46.8
1987	-13.92	4.16	-30.7	10.7	0.5	-1.5

compare differences in persistency between the RPM and RR-TDM, young bulls were grouped for persistency and again compared based on the EBV at the age of 4.5 and 6 years old. The genetic production on day 280 minus day 60, as suggested by Jamrozik et al. (1998), was used as measure for persistency (p280-p60). When average 305-d EBVs of young bulls are compared based on their persistency differences were larger (i.e., a sire with a smaller difference for p280-p60 than the average sire was assumed to be more persistent and the other way around). For the more persistent young bulls (Table 1, column 4 and 5) the RPM showed a larger increase in average 305-d EBV compared to the RR-TDM. For the less persistent young bulls differences between the model were relatively small. This suggest that the RR-TDM predict EBVs of more persistent bulls better.

Summary

Thesis Overview

Test-day models (**TDM**), or the modeling of time or age dependent traits in general, is obtaining increasing attention (e.g., Ali and Schaeffer, 1987; Kirkpatrick et al. 1994; Schaeffer and Dekkers, 1994; Meyer and Hill 1997; and Pletcher and Geyer, 1999). Adding time into the model as a dependent factor for production traits makes sense when one wants to predict an animals production characteristics over a period of time beforehand, i.e., to predict reliable and accurate EBVs as soon as possible to optimize the genetic gain and generation interval. Milk production of dairy cows is such a trait that changes over time; after calving a cow's production first increases until peak around day 60, decreases steadily after that depending on its persistency and is influenced by genetic and environmental effects. The current model for breeding values estimation of dairy cattle in the Netherlands is by a lactation model based on realized or projected 305-d lactation yields. Switching over from a lactation yield based model into a single test-day based model (i.e., a TDM) models besides the level of production also the shape of the lactation curve over days in milk (**DIM**). This thesis describes the choices and decisions made to develop a TDM and were based on Dutch dairy cattle data.

In chapter 2 and 3, the choice for the random regression approach (**RR**) TDM and which lactation function to chose were discussed. Ptak and Schaeffer (1993) described a repeatability model, which assumed that milk production on different DIM was a measure of the same, repeated trait. Wiggans and Goddard (1996) describe a multiple-trait TDM and reduced the number of parameters by a canonical transformation. Although it allows correlations between DIM to be less than one, information from the ordering of test-day records is not used and estimates of the full covariance matrix are needed beforehand. Two other approaches, Covariance Functions (Kirkpatrick et al., 1994) and RR-TDM (Schaeffer and Dekkers, 1994) use a function to model lactation records. Covariance functions model an infinite number of age traits to describe the underlying covariance structure in the data, and RR-TDMs model the shape of the lactation curve with a function directly from the data. Both methods are equivalent if linearized functions are used (Meyer, 1998).

To chose the correct lactation function in a RR-TDM we started of with a phenotypic model and fitted: i) an overall level as in a lactation model; ii) a level and a slope, because visually the lactation curve looks like a line; iii) the Wilmink lactation curve (Wilmink 1987a; used for extension of part-lactations); iv) a spline-function (based on two functions, one that describes the increase until peak and one the decline thereafter); and v) several higher order

87

Legendre polynomials (Kirkpatrick et al, 1994). Model parameter estimates were expressed as correlations and mean square errors of predictions (**MSEP**) and compared for different sets of part lactations. When the lactation function was modeled as a line the variance and correlation structure fitted was systematically different (Chapter 3: Figures 3 and 4), from which we concluded that higher orders of fit were necessary. When Legendre polynomials are used as the lactation function, model parameters are normalized and standardized for time, which improved convergence and ensure more accurate results than with conventional polynomials. Overall, a sixth order Legendre polynomial [LEG(5)] yielded the best fit. Because, variance estimates of milk yield for days at the ends of the lactation curve were inaccurate, it was suggested to use more complete lactation data.

Chapter 4 describes the use of more complete data (i.e., lactations with at least 22 weekly tests and last test-day at or after day 280 DIM) and a correction for heterogeneous variance among DIM as suggested by Meuwissen et al. (1996). Both effects enabled a reduction of the least order of fit. Based on more complete data LEG(4) was sufficient and with an additional correction for heterogeneous variances the goodness of fit of LEG(3) was sufficient. Although, more complete data may have introduced some selection bias (e.g. omitting of poor producing cows), the possible bias seemed to have only little effect on the observed variances for daily milk yields and the MSEP even improved. Because a correction of heterogeneity of variance increased computing time considerably, at this stage, it was suggested to apply the correction only for the prediction of EBVs and not for parameter estimation.

In chapter 5 genetic parameters of a RR-TDM for first lactation records were presented. Because computing capacity is limited and memory required of deterministic variance component estimation programs based on direct solving of the mixed-model equations was too large, a Gibbs-sampling procedure based on Bayesian-inference was implemented. The lactation curve was modeled by a fifth order Legendre polynomial [LEG(4)] for both the genetic and permanent environmental effects. Test-day records from 23.700 complete lactations (i.e., at least six milk recordings, an average test-day interval of at maximum 50 d, at least one test-day record at or before day 80, and one at or after day 280) of 475 herds were used. The covariance structure expected by the RR-TDM was compared to bi-variate estimates (30-d intervals) and showed that for the genetic part a fourth order Legendre polynomial [LEG(3)] was sufficient, but for the permanent environmental part a fifth order of fit [LEG(4)] was necessary.

In chapter 6 the RR-TDM was extended from a single trait model into a multiple-trait model for first, second and third lactations as different and independent traits. The number of parameters to be estimated per animal increased from 10 to 30 parameters (i.e., covariance

88

functions of dimension 15). But such large models are computationally hard to solve, often overparameterized and certainly not parsimonious. To reduce the number of parameters a stepwise reducing rank procedure, described by Misztal et al. (2000), was applied. In each round: covariance functions were reduced by setting the lowest eigenvalues equal to zero (i.e., if the relative value was less than 2%); random regression coefficients were converted to the new scale; information of other traits was added; and covariance functions had to be re-estimated. After a final step of reduction, variance curves expected among DIM and correlations expressed between DIM for the different lactations showed a good fit. Overall, the number of parameters could be halved without reducing the goodness of fit considerably and the procedure was recommended to extend the RR-TDM further for milk, fat and protein.

In the general discussion (chapter 8) a single trait RR-TDM and a repeatability TDM were applied to compare average breeding values (**EBVs**) for different groups of animals and for young bulls based on different amounts of information (i.e., running or completed lactations for first versus second crop daughters). Correlations of EBVs between models were high but less than one and standard deviations of EBVs were slightly higher for the RR-TDM. For 305-d productions, the genetic trend of young bulls (grouped by birth year) was 106 kg of milk per year in the repeatability model and 94 kg of milk in the RR-TDM. However, the genetic merit of an animal expressed by the RR-TDM provides more information than from the repeatability model; it also describes the shape of the lactation curve from which EBVs for persistency can be derived easily. EBVs for sires with more persistent daughters from the RR-TDM seemed to fluctuate less than from the repeatability model. Based on the genetic merit curves of the RR-TDM selection in the past has been for overall level and not for the shape of the lactation curve, which did not change at all. With the introduction of a RR-TDM large differences in the ranking of sires are not expected, genetic gain for 305d production would be slightly lower, but differences expressed for persistency by the RR-TDM will allow selection for the shape of the lactation curve.

Recent Developments

The TDM presented in this thesis reflexes the current state of research and is open for changes and improvements. For example, until now, the residual term was modeled as the measurement error and therefore assumed constant across DIM. However, if classes for residual variances are modeled across DIM [e.g. discussed by Olori et al. (2000)] the residual variance estimates are high at the beginning of lactation, decreases over DIM with and tend to increase again at the end the trajectory. Olori et al. (1999) concluded that not the number and length of the residual classes did matter, but the precise subdivision into residual classes. Preliminary results (not shown) of including 10 residual term classes in the multiple-trait RR-TDM, as described in chapter 6, indicated a comparable trend for the residual variances across

DIM. However, the increase of residual variances at the beginning of lactation seemed to be compensated in the permanent environmental part. Although the subdividing of residual term into several classes seemed to be a redistribution of the amount of variance between the residual and permanent environmental part, it could act as a correction for heterogeneity of variance for permanent environment and might be possible to reduce the order of fit of the permanent environmental part in the RR-TDM.

Accounting for heterogeneous variance among DIM seems to be the next step in order to disentangle the estimation of both the covariance and correlation structure at the same time. Because, not only the shape of the variance curve defines the goodness of fit of the covariance function used in the RR-TDM, it depends also on the curvature of correlations between test-days yields across DIM. As already discussed in chapter 4, the correction for heterogeneous variance of milk yield across DIM by joint estimation of EBVs and heterogeneous variances (Meuwissen et al., 1996), scaled the observed variances towards the variances expected by the model. Hence, the goodness of fit of random regression part of the TDM was no longer based on the (co)variances but only the correlations between the test-days and due to that a reduction of at least one order of fit was possible. However, the computational demand of applying such a correction was relatively large compared to the gain in order of fit and MSEP. The "constructive approach", described by Misztal et al. (2000), and the character process, described by Pletcher and Geyer (1999) and presented by Jaffrézic and Pletcher (2000), are all based on separated modeling of the covariance and correlation structure. Those methods have the advantage that the number of parameters to be estimated is considerably lower than for RR-TDM with a high order of fit. However, in the constructive approach the structure underlying the data is a RR-function while the character process approach is based on modeling the covariance and correlation structure explicitly without using RR-functions, which means that it not easy to predict the EBVs for such a model. Another possibility to correct for heterogeneous variance of milk yield across DIM would be by including a scaling factor into the random regression part of the RR-TDM which is estimated interactively during parameter estimation. Although test-day models seem to be a good tool for genetic evaluation of dairy cattle, they are still subject to development and will probably remain under continuously improvement.

Samenvatting

Algemene inleiding

In de veefokkerij worden dieren vergeleken op basis van hun fokwaardes (genetische waarde) om zo de genetische aanleg van een groep dieren (populatie) in de gewenste richting te verbeteren voor de (productie)kenmerken die in het fokdoel beschreven staan. Voor de Nederlandse rundmelkvee populatie verzorgt het NRS (Nederlands Rundvee Syndicaat) onder toezicht van het NVO (de Nederlandse Veeverbeterings Organisaties) viermaal per jaar de fokwaardeschatting, waarbij de productiegegevens van 1.3 miljoen dieren (ruim 81% van de Nederlandse melkveestapel) wordt meegenomen.

Met het uitrekenen van een fokwaarde voor een dier wordt een inschatting gemaakt van de genetische waarde, c.q. potentie van dat dier ten opzicht van een vooraf gedefinieerde basis. De basis wordt gevormd door het gemiddelde van alle dieren geboren in een bepaald jaar. In Nederland staat deze voor een langere periode vast (een vaste basis), maar het kan bijvoorbeeld ook het gemiddelde van een x-aantal jaren terug zijn (een rollende basis). Voor de fokwaardeschatting worden de dieren vergeleken op basis van hun eigen prestaties (productiegegevens), die van groepsgenoten en die van verwanten. Als de prestaties van een dier wordt vergeleken met die van de groepsgenoten (die dieren die onder dezelfde milieuomstandigheden hebben geproduceerd) spreken we van een phenotypische vergelijking en als er ook rekening wordt gehouden met de afstammingsgegevens van het dier (verwantschappen tussen dieren) dan spreken we van een genetische vergelijking. De genetische vergelijking maakt dus een inschatting van de genetische potentie van een dier door rekening te houden met de genetische relaties tussen dieren en gelijktijdig te corrigeren voor de omgeving waarin het zich bevindt, met andere woorden er wordt een schatting gemaakt van wat een dier op basis van zijn of haar genetische aanleg zou kunnen produceren en dat noemen we de fokwaarde. Dus als we een fokwaarde voor een dier uitrekenen, hebben we een schatting voor hoe goed of hoe slecht een dier is of zal zijn voor de gewenste (productie)kenmerken en weten we ook of het dier wel of niet interessant is om geselecteerd te worden als ouderdier om er de volgende generatie mee te fokken. Immers, de verwachtingswaarde van een nakomeling van de geselecteerde ouderdieren is gemiddeld gezien even hoog als het gemiddelde van hun ouders (namelijk, een dier vererft de helft van de genen van de moeder en de andere helft de vader). Dus als de geselecteerde (ouder)dieren gemiddeld een betere fokwaarde hebben dan het gemiddelde van de populatie, dan zal het gemiddelde van de nakomeling (de nieuwe populatie) in de volgende generatie hoger zijn dan voor de huidige generatie en is de genetische aanleg van de populatie verbeterd.

De snelheid waarmee deze vooruitgang wordt gerealiseerd is afhankelijk van meerdere factoren. Ten eerste is dat de erfelijkheid van het kenmerk; de mate waarin het kenmerk wordt bepaald door de genen. Het kengetal dat we hiervoor gebruiken is de erfelijkheidsgraad (h^2) en geeft aan in welke mate wij de in de data waargenomen variatie kunnen verklaren aan de hand van genetische verschillen tussen dieren. Ook het generatie-interval (de gemiddelde leeftijd van de ouderdieren bij kalven) en de selectie-intensiteit (selectiedruk) zijn van invloed op de snelheid waarmee de genetische vooruitgang kan worden gerealiseerd. Zo is het generatie interval bij melkvee voor koeien om koeien te fokken 3 à 4 jaar en voor stieren om stieren te fokken 5 à 6 jaar lang. Bij het varken is het generatie-interval daarentegen korter (± 1 jaar) want het varken is eerder geslachtsrijp en heef een kortere voortplantingscyclus. Bovendien is het aantal nakomelingen per dier groter (meerdere worpen per jaar met meerder nakomelingen per worp) en is er een hogere selectie-intensiteit omdat er scherper geselecteerd kan worden. De genetische vooruitgang bij het varken is dan ook hoger en sneller te realiseren dan bij het rund.

Naast de snelheid waarmee de genetische vooruitgang wordt gerealiseerd is ook de mate van genetische variatie dat voor een kenmerk in de populatie aanwezig is van belang. Zijn er weinig genetische verschillen tussen dieren voor de (productie)kenmerken dan zal de genetische spreiding klein zijn en zal er strenger geselecteerd moeten worden en duurt het dus langer (meerdere generaties) om dezelfde genetische vooruitgang te behalen. In deze zin is ook de mate van verwantschap tussen dieren (inteelt) van belang. Immers als de kans dat 'twee allelen voor een gen (één van de moeder en één van de vader) identiek zijn door afstamming' groter is dan door toeval dan zijn de dieren ingeteeld. Dit betekent dat de ouderdieren meer op elkaar lijken dan twee willekeurige dieren uit de populatie en dat de verschillen tussen de geselecteerde dieren daardoor kleiner zullen zijn en de selectie mogelijkheden dus beperkt.

Van een correcte fokwaardeschatting wordt verwacht dat de fokwaarde van een dier stabiel blijft als er in de loop van de tijd meer informatie omtrent het dier beschikbaar komt, zodat het verschil tussen de verwachte genetische vooruitgang en het uiteindelijk gerealiseerd selectieverschil (genetische vooruitgang) zo klein mogelijk is. Om er zeker van te zijn dat de juiste dieren worden geselecteerd hebben fokkerijorganisaties fokprogramma's opgezet waarin koeien met de hoogste verwachting worden getoetst op speciale testbedrijven (onder dezelfde omstandigheden) en worden stieren eerst in de praktijk uitgetest alvorens ze het predikaat fokstier krijgen. Om juiste voorspellingen te kunnen doen en ervoor te zorgen dat de verwachte vooruitgang ook daadwerkelijk wordt gerealiseerde, moet de betrouwbaarheid (de hoeveelheid informatie) en nauwkeurigheid (de precieze) waarmee fokwaarden worden geschat voldoende hoog zijn. Immers onvolledige data en onnauwkeurigheden (c.q.

tekortkomingen) in de methode geven dat fokwaarden zullen variëren waardoor het beoogde selectieresultaat niet behaald wordt en er dus een lagere genetische vooruitgang zal worden gerealiseerd wat hoge kosten met zich meebrengt.

Dit proefschrift

De in dit proefschrift beschreven studies zijn bedoeld om de huidige methode van fokwaardeschatting uit te breiden en verder te volmaken. De huidige fokwaardeschatting is een lactatiemodel waarbij dieren worden vergeleken op basis van de gerealiseerde c.q. voorspelde 305-dagen (lactatie)producties. De methode is in feite een twee-staps procedure. In stap 1 worden de 305-dagen producties berekend aan de hand van de individuele proefmelkingen door deze volgens standaardproductiecurves te sommeren tot één getal voor de gehele lactatieperiode, of er wordt een voorspelling gemaakt als de productiegegevens onvolledig of (nog) niet bekend zijn. Alle afzonderlijke proefmelkgegevens worden dus gesommeerd tot één waarde, de 305-dagen productie. Stap 2 is de feitelijke fokwaardeschatting waarin de dieren onderling worden vergeleken in. In stap 2 is dus geen informatie meer bekend over de afzonderlijke proefmelkingen, zoals het aantal, de lengte van de intervallen tussen opeenvolgende proefmelkingen en het effect van de dag waarop de proefmelking heeft plaatsgevonden. In de huidige methode wordt namelijk aangenomen dat het aantal proefmelkingen waarop een 305-dagen productie is gebaseerd voor alle dieren gelijk is, maar in de praktijk is het aantal echter variabel waardoor de betrouwbaarheid van de fokwaardeschatting eigenlijk wordt ondermijnd. Ook is het gewenst om te corrigeren voor de dag van proefmelking, immers het effect van een regenachtige dag of een verandering in het rantsoen zal de productie van de dieren op de dag van proefmelking wel beïnvloeden en is niet een direct gevolg van genetische verschillen tussen dieren, maar wordt veroorzaakt door (storende) omgevingsfactoren waarvoor we moeten corrigeren. Bovendien geeft de huidige fokwaardeschatting geen informatie voor een kenmerk als persistentie welke het verloop van de productiecurve in de tijd weergeeft en kunnen we dus ook niet voor de vorm van de productiecurve selecteren.

In plaats van één waarneming voor de gehele lactatieperiode te gebruiken (de 305-dagen productie) kunnen de onderliggende individuele proefmelkgegevens ook direct in de fok-waardeschatting worden gebruikt. Een dergelijk model wordt een Test Dag Model genoemd en geeft naast een schatting voor het productieniveau ook informatie over het verloop van de productiecurve van een dier. Om de genetische verschillen in het verloop van de productiecurve tussen dieren te kunnen beschrijven is het nodig om voor ieder dier een afzonderlijk curve te fitten (bijv. met een regressie-analyse op dagen in melk, **DIM**). In een Test Dag Model waarbij een functie wordt gebruik om de vorm van de productiecurve van ieder individueel dier te beschrijven ten opzicht van een gemiddelde productiecurve is voor

melkvee door Schaeffer en Dekkers (1994) geïntroduceerd en staat bekend als een Random Regressie Test Dag Model. Canada past het Test Dag Model sinds 1999 toe en is het eerste land dat een dergelijk model gebruikt voor de officiële fokwaardeschatting. Ook Finland heeft onlangs in 2000 het Test Dag Model geïntroduceerd. Duitsland en Nieuw Zeeland passen wel een correctie toe voor de dag van proefmelking maar houden nog geen rekening met verschillen tussen dieren in het verloop van de productiecurve omdat iedere proefmelking als een herhaalde waarneming van hetzelfde kenmerk worden beschouwd. Dit is in tegenstelling tot het Random Regressie Test Dag Model waar opeenvolgende proefmelkingen wel als verschillende kenmerken worden beschouwd en correlaties tussen opeenvolgende test dagen (proefmelkingen in verschillende lactatiestadie) worden meegenomen om het model zo van informatie te voorzien omtrent de vorm van de productiecurve voor elk individueel dier.

Echter het gebruik van de individuele proefmelkgegevens rechtstreeks in de fok-waardeschatting is een forse uitbreiding van het model, namelijk van één waarneming per dier in het lactatiemodel (de 305-dagen productie) naar meerdere proefmelkingen (6-10 test dagen) per dier in het Test-Dag-Model. Om een Test Dag Model te kunnen draaien is dus veel computercapaciteit nodig. Maar de huidige stand van computertechnologie en gezien de zeer snelle ontwikkelingen in de computerbranche wordt de toepassing van Test Dag Modellen in de praktijk een steeds meer voor de handliggende optie.

Het proefschrift begint met een algemene inleiding. In de hoofdstukken 2 en 3 is gekeken met welke (lactatie)functie het verloop van de productie (de vorm van de productiecurve) het beste kan worden beschreven. Als productiegegevens van een dier in een grafiek worden uitgezet tegen het lactatiestadium, dan lijkt het of de productiecurve vrij eenvoudig kan worden beschreven door een gemiddelde dagproductie (het niveau) en een gestage, maar constante afname (als een lijn) na het bereiken van de piekproductie (rond dag 60 in de lactatie).

Het eerste model [LEVEL of LEG(0)] beschrijft de productie met maar één term en kan dus alleen een verwachting geven van de gemiddelde dagproductie van een dier (het niveau). De gemiddelde dagproductie geschat in dit model komt min of meer overeen met de 305-dagen productie in het huidige lactatiemodel en is dan ook als een referentiemodel gebruikt. Model LEVEL is weliswaar een Test Dag Model en geen lactatiemodel. De individuele proefmelkingen worden in het model LEVEL wel gebruikt om voor de dag van proefmelking te corrigeren, maar geven geen informatie over verschillen tussen producties op verschillende lactatiestadia omdat alle proefmelkingen als waarnemingen van één en hetzelfde kenmerk worden beschouwd. Model LEVEL is dus in feite een herhaalbaarheidsmodel en is vergelijkbaar met het Test Dag Model zoals het in Duitsland is toegepast. Het tweede model [LINE of LEG(1)] bevat naast een term voor het niveau ook een term die het verloop van de

curve beschrijft. Het gebruikt hiervoor de richtingscoëfficiënt van een lijn en kan dus wel rekening houden met verschillen in de vorm van de productiecurve tussen dieren. In alle overige modellen zijn steeds hogere orde termen opgenomen om de lactatiefunctie nog flexibeler te laten zijn (DIM^2, DIM^3, … DIM^7). Naast het modelleren van de productiecurve met een regressie op dagen in melk zijn ook Legendre polynomen (LEG) gebruikt. Een model met LEG geeft dezelfde oplossingen als bij een rechtstreekse regressie op DIM maar heeft als voordeel dat het model gemakkelijker en sneller is op te lossen.

Uit de resultaten blijkt dat een lijn [model LIJN of LEG(1)] als lactatiefunctie de waargenomen verschillende tussen dieren in de data niet voldoende goed kan beschrijven. De oorzaak hiervoor is de wijze waarop verschillen tussen dieren in de fokwaardeschatting worden gemodelleerd. Zoals gezegd lijkt het dat de productiecurve kan worden gemodelleerd met een functie die de gemiddelde dagproductie en een constante afname na de piek beschrijft. Echter in de fokwaardeschatting wordt niet de vorm van de productiecurve gemodelleerd, maar de onderliggende variatie die de onderlinge verschillen tussen dieren in de data verklaart. Om deze variantiestructuur correct te modelleren in de fokwaardeschatting kan niet worden volstaan met een eenvoudig functie als een lijn, maar zijn hogere orde termen voor nodig (meer flexibiliteit). Een kenmerk als persistentie is dus niet simpel te beschrijven met een lijn.

De juiste orde of fit (het aantal termen in de lactatiefunctie) is vastgesteld door ontbrekende records van deellactatie te voorspellen, waarbij de lengte van de deellactatie is gevarieerd. Op basis van deze voorspellingen blijkt dat minimaal een 4^e orde polynoom nodig is voor een goede weergave van het verloop van de productiecurve. Het aantal parameters dat dan per dier geschat moet worden is minimaal 5 en maakt dat het totaal aantal te schatten parameters (voor alle dieren) groot is.

In hoofdstuk 4 en later ook hoofdstuk 6 zijn mogelijkheden beschreven om het aantal parameters terug te brengen en zo de omvang van een Test Dag Model te reduceren. Enerzijds vanwege de vereiste computercapaciteit en anderzijds om de complexiteit van het model en de kans op overparametersering terug te brengen.

Het aantal proefmelkingen waaruit een productiecurve is opgebouwd en dan met name hoe volledig en hoe goed deze zijn verdeeld over de gehele productieperiode blijkt een belangrijke rol te spelen op een correcte fit van het model. Op basis van alleen volledige gerealiseerd productiegegevens (dus over de gehele 305 dagen periode bekend) blijkt dat de orde of fit met één term kan worden teruggebracht. Een tweede reductie van één orde of fit is mogelijk als een correctie van heterogeniteit van variantie voor dagen in melk wordt toegepast. Doormiddel van deze correctie wordt er gecorrigeerd voor verschillen in variatie van productiegegevens op verschillen lactatiestadia. Echter, de reductie van één order of fit weegt nauwelijks op tegen de extra computertijd die hiervoor nodig is.

In hoofdstuk 5, is het Test Dag Model uitgebreid van een phenotypisch model naar een genetisch model. Dit betekent dat er voor zowel de omgevingsfactoren (permanent milieu) als het genetische deel, ieder afzonderlijk een lactatiefunctie moet worden opgenomen. Het aantal model parameters verdubbelt hier dus wel door. Voor het schatten van de genetische model parameters zijn de gegevens van 23.700 dieren meegenomen. De omvang van zo'n model is dusdanig groot dat standaardprogrammatuur voor het oplossen van de vergelijking niet meer toereikend waren en eigen programmatuur moest geschreven worden waarbij gebruik is gemaakt van Gibbs-sampling technieken om de vergelijkingen op te lossen.

De volgende stap was (hoofdstuk 6) was een uitbreiding van het Test Dag Model van één kenmerk naar meerdere kenmerken. Immers de melkproductiecurve in de eerste lactatie verschilt in zowel het niveau als het verloop ten opzichte van tweede en latere lactaties en zijn dus eigenlijk verschillende (productie) kenmerken welke als zodanig gemodelleerd moeten worden. Deze uitbreiding van een single-trait model (één kenmerk) naar een multi-trait model (meerdere kenmerken) betekent wel een verdubbeling van het aantal model parameters voor ieder extra kenmerk. Om te voorkomen dat het model zo groot wordt dat de parameters niet meer of zeer moeilijk te schatten zijn en om ervoor te zogen dat het model binnen de beschikbare computercapaciteit blijft is gezocht naar een manier waarbij de goodness of fit (juistheid van het model) gehandhaafd blijft, maar het aantal parameters sterk teruggebracht wordt. Door de informatie van de verschillende lactaties stapsgewijs in het model op te nemen en tussentijds het aantal parameters in het model te reduceren (te her-parameteriseren met behulp van reduced rank technieken en met alleen die kenmerken verder te gegaan welke veel variatie verklaren) is het aantal parameters met de helft terug te brengen. Deze methode is gesuggereerd door Misztal et al. (2000) en uitgewerkt in dit proefschrift aan de hand van twee alternatieven.

In dit proefschrift is alleen gekeken naar de melkproductie. Voor een verdere uitbreiding van het Test Dag Model naar een model voor zowel de melk-, vet- als eiwitproductie als drie verschillende kenmerken wordt de stepwise-reduced rank procedure gesuggereerd.

In het laatste hoofdstuk (7) zijn de fokwaarden van een 4^e order of fit Random Regressie Test Dag Model (**RR-TDM**) vergeleken met een 0^e orde fit model [het herhaalbaarheidsmodel (**RPM**), wat vergelijkbaar is verondersteld met het huidige lactatiemodel). De trend in fokwaardes voor stieren was 94 kg melk per jaar in het RR-TDM en iets lager dan in het herhaalbaarheidsmodel, namelijk 106 kg per jaar. Als de curves met fokwaarden voor meerdere jaargangen proefstieren worden uitgezet tegen het lactatiestadium blijkt dat deze wel verschillen in het niveau maar voor in de vorm van de productiecurve., Dit betekent dat selectie in het verleden wel voor niveau is geweest maar niet voor vorm van de lactatiecurve.

De correlaties tussen fokwaarden voor verschillende groepen dieren geschat met beide modellen waren hoog en fokwaarden in het RR-TDM vertoonden een iets hogere spreiding wat op iets hogere selectiemogelijkheden voor het RR-TDM duidt. Verder zien we dat de fokwaarden voor stieren met meer persistente dochters in het RR-TDM minder variëren dan in het RPM als er meer informatie van een dier in de loop van de tijd beschikbaar komt.

De uitbreiding van het lactatiemodel naar een 4^e order of fit Random Regressie Test Dag Model is een forse uitbreiding voor wat de vereiste computercapaciteit betreft, maar heeft als voordeel dat er naast het niveau van de productie ook fokwaardes berekend kunnen worden voor een kenmerk als persistentie. Verder is het niet langer meer nodig om voorafgaande aan de fokwaardeschatting eerst de 305-dagen producties te bereken of te voorspellen. Bovendien corrigeert het Test Dag Model voor het effect van de dag van proefmelking, houdt het rekening met het aantal proefmelkingen, de volgorde en de lengte van de intervallen daartussen. Verwacht wordt dat de volgorde van stieren bij de fokwaardeschatting niet drastisch zal veranderen en dat de fokwaarde van stieren met meer persistente dochters stabieler zal worden.

References

Ali, T. E., and L. R. Schaeffer. 1987. Accounting for covariances among test day milk yields in dairy cows. *Canadian Journal of Animal Science* **67**: 637-644.

Batra, T. R., C. Y. Lin, A. J. McAlister, and A. J. Lee. 1987. Multi-trait estimation of genetic parameters of lactation curves in Holstein heifers. *Journal of Diary Science* **70**: 2105-2111.

Cobby, J. M., and Y.L.P. Le Du. 1978. On fitting curves to lactation data. *Animal Production* **26**: 127-133.

Danell, B. 1982. Studies on lactation yield and individual test-day yields of Swedish dairy cows. 4. Extension of part-lactation records for use in sire evaluation. *Acta Agricculturae Scandinavica*. **32**: 103-114.

Dommerholt, J. 1975. *Correctie van de melkgift van koeien voor verschillen in leeftijd, seizoen en lactatiestadium.* Agricultural university Wageningen, Wageningen, The Netherlands, thesis.

Dommerholt, J. 1979. De produktievererving van stieren in netto melkgeld. *De Friese Veefokkerij* **2**: 106-110.

Elston, D. A., C. A. Glasbey, and D. R. Neilson. 1989. Non-parametric lactation curves. *Animal Production* **48**: 331-339.

Gelfand, A. E., and A.F.M. Smith. 1990. Sampling based approaches to calculating marginal densities. *Journal of American Statistical Association* **85**: 398-409.

Geman, S., and Geman, D. 1984. Stochastic relaxation, Gibbs distributions and the Bayesian restoration of images. *IEEE Transactions on Pattern Analysis and Machine Intelligence* **6**: 721-741.

Gengler, N. 1996. Persistency of lactation yield: a review. *Proceedings international workshop on genetic improvement of functional traits in cattle.* Gembloux, Belgium.

Gilmour, A. R., R. Thompson, B. R. Cullis, and S. J. Welham. 1999. *ASREML. Reference Manual*, NSW Agriculture, Orange, 2800, Australia. ftp: ftp.res.bbsrc.ac.uk in pub/aar.

Grossman, M. and W. J. Koops. 1988. Multiphasic analysis of lactation curves in dairy cattle. *Journal of Diary Science* **71**: 1598-1608.

Guo, Z., and H. H. Swalve. 1995. Modeling of the lactation curve as a sub-model in the evaluation of test day records. INTERBULL Open Meeting, Pruhonice, Prague, September 7-8. *Bulletin* **11** (4 pages). International Bull Evaluation Service, Uppsala, Sweden.

Guo, Z., and H. H. Swalve. 1997a. Comparison of different lactation curve sub-models in test day models. INTERBULL Open Meeting, Vienna, Austria, August 28-29. Pages 75-79 in *Bulletin* **16**. International Bull Evaluation Service, Uppsala, Sweden.

Guo, Z., and H. H. Swalve. 1997b. Modeling the lactation curve with interpolation and B-splines. *Proceedings of European Association for Animal Production 48th Annual Meeting,* Vienna, Austria, August 25-28. Page 55. Wageningen Pers, Wageningen, The Netherlands.

Harville, D. A. 1974. Bayesian inference for variance components using only error contrasts. *Biometrika* **61**: 383-385.

Henderson, C. R. 1948. *Estimation of general, specific, and maternal abilities*. Iowa State University, Iowa, USA, thesis.

Henderson, C. R. 1973. Sire evaluation and genetic trends. *Proceedings of the Animal Breeding and Genetics Symposium in honor of Dr. J.L. Lush.* University of Guelph**,** Guelph, ON, Canada, pages 10-41.

Henderson, C. R. 1984. *Applications of linear models in animal breeding*. University of Guelph, Guelph, ON, Canada. pages 196-206.

Jaffrézic, F., and S. D. Pletcher. 2000. Statistical models for the genetic analysis of repeated measurements. *Proceedings of the European Association for Animal Production 51**-**th Annual Meeting*, Den Hague, The Netherlands, August 21-24. Page 94. Wageningen Pers, Wageningen, The Netherlands.

Jamrozik, J, and L. R. Schaeffer. 1997. Estimation of genetic parameters for a test day model with random regressions for yield traits of first lactation holsteins. *Journal of Dairy Science* **80**: 762-770.

Jamrozik, J., G. Jansen, L. R. Schaeffer, and Z. Liu. 1998. Analysis of persistency of lactation calculated from a random regression test day model. INTERBULL Open Meeting, Rotorua, New Zealand, January 18-19. Pages 60-61 in *Bulletin* **17**. International Bull Evaluation Service, Uppsala, Sweden.

Jamrozik, J., G. J. Kistemaker, J.C.M. Dekkers, and L. R. Schaeffer. 1997a. Comparison of possible covariates for use in a random regression model for analysis of test day yields. *Journal of Dairy Science* **80**: 2550-2556.

Jamrozik, J., L. R. Schaeffer, and J.C.M. Dekkers. 1996. Random regression models for production traits in Canadian Hol-steins. INTERBULL Open Meeting., Veldhoven, the Netherlands, June 23-24. Pages 124-134 in *Bulletin* **14**. International Bull Evaluation Service, Uppsala, Sweden.

Jamrozik J., L. R. Schaeffer, and J.C.M. Dekkers. 1997b. Genetic evaluation of dairy cattle using test day yields and random regression model. *Journal of Dairy Science* **80**: 1217-1226.

Jamrozik, J., L. R. Schaeffer, Z. Liu, and G. Jansen. 1997c. Multiple trait random regression test day model for production traits. INTERBULL Open Meeting, Vienna, Austria, August 28-29. Pages 43-47 in *Bulletin* **16**. International Bull Evaluation Service International Bull Evaluation Service, Uppsala, Sweden.

Jansen, J., J. Dommerholt, and W.M.G. Wigmans. 1983. *Breeding values for milk production traits in the Netherlands.* Report B-211, Department of Animal Breeding, Agricultural University Wageningen, Research Institute for Animal Production "Schoonoord", and Central Milk recording Service, The Netherlands.

Janss, L.L.G, and G. de Jong. 1999. MCMC based estimation of variance components in a very large dairy cattle data set. INTERBULL, International Workshop on High Performance Computing and New Statistical Methods in Dairy Cattle Breeding, Tuusula, Finland, March 28-29. Pages 63-68 in *Bulletin* **20**. International Bull Evaluation Service, Upsala Sweden.

Kettunen, A., E. A. Mäntysaari, I. Strandén, J. Pösö, and M. Lidauer. 1998. Estimation of genetic parameters for first lactation test day milk production using random regression models. *Proceedings of the 6th World Congres on Genetics Applied to Livestock Production.* Armidale, New South Wales, Australia **23**: 307-310.

Kirkpatrick, M., W. G. Hill, and R Thompson. 1994. Estimating the covariance structure of traits during growth and ageing, illustrated with lactation in dairy cattle. *Genetical Research Cambridge*. **64**: 57-69.

Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* **124**: 979-993.

Kistemaker, G. J., and L. R. Schaeffer. 1998. Adjustment for heterogeneous Herd-Test-Day variances. INTERBULL Meeting., Rotorua, New Zealand, January 18-19. Pages 55-59 in *Bulletin* **17**. International Bull Evaluation Service, Upsala Sweden.

Koenen, E.P.C., and R. F. Veerkamp. 1998. Genetic covariance functions for live weight, condition score, and dry-matter intake measured at different lactation stages of Holstein Friesian Heifers. *Livestock Production Science* **57**: 67-77.

Lidauer, M., E. A. Mäntysaari, I. Strandén, and J. Pösö. 2000. Multiple-trait random regression test-day model for all lactations. INTERBULL Open Meeting., Bled, Slovenia, May 14-15. Pages 81-86 in *Bulletin* **25**. International Bull Evaluation Service, Uppsala, Sweden.

Liu, Z., J. Jamrozik, and G. Janssen. 1998. A comparison of fixed and random regression models applied to dairy test day production data. INTERBULL Open Meeting, Rotorua, New Zealand, January 18-19. Pages 60-61 in *Bulletin* **17**. International Bull Evaluation Service, Uppsala, Sweden.

Mäntysaari, E. A. 1999. Derivation of multiple trait reduced rank random regression model for the first lactation test-day records of milk, protein and fat. *Proceedings of European Association for Animal Production 50th Annual Meeting,* Zurich, Switzerland, August 22-26. Page 26. Wageningen Pers, Wageningen, The Netherlands.

Masselin, S., D. Sauvant, P. Chapoutot, and D. Milan. 1987. Les modèles d'ajustement des courbes de lactation. *Annales de Zootechnie* **36**: 171-206.

Meuwissen T.H.E., G. de Jong, and B. Engel. 1996. Joint estimation of breeding value and heterogeneous variances of large data files. *Journal of Dairy Science* **79**: 310-316.

Meyer, K. 1997. An 'average information' restricted maximum likelihood algorithm for estimating reduced rank genetic covariance matrices or covariance functions for animal models with equal design. *Genetics, Selection and Evolution* **29**: 97-116.

Meyer K. 1998. Estimating covariance functions for longitudinal data using a random regression model. *Genetics, Selection and Evolution* **30**: 221-240.

Meyer, K., H. U. Graser, and K. Hammond. 1989. Estimates of genetic parameters for first lactation test day production of Australian black and white cows. *Livestock Production Science* **21**: 177-199.

Meyer K., and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. *Livestock Production Science* **47**: 85-200.

Misztal, I., T. Strabel, J. Jamrozik, E. A.. Mäntysaari, and T.H.E. Meuwissen. 2000. Strategies for estimating the parameters needed for different test-day models. *Journal of Dairy Science* **83**: 1125-1134.

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. *Livestock Production Science* **61**: 53-63.

Pander, B. L., W. G. Hill, and R. Thompson. 1992. Genetic parameters for test day records of British Holstein-Friesian heifers. *Animal Production* **55**: 11-21.

Patterson, H. D., and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**: 545-554.

Pérochon L., J. B. Coulon, and F. Lescourret. 1996. Modelling lactation curves of dairy cows with emphasis on individual variability. *Animal Science (Pencaitland)* **63**: 189-200.

Pool, M. H., and T.H.E. Meuwissen. 1999. Prediction of daily milk yields from a limited number of test days using test-day models. *Journal of Dairy Science* **82**: 1555-1564.

Pool, M. H., and T.H.E. Meuwissen. 2000. Reduction of the number of parameters needed for a polynomial random regression test-day model. *Livestock Production Science* **64**: 133-145.

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

Pletcher, S. D., and C. J. Geyer. 1999. The genetic analysis of age-dependent traits: modeling the character process. *Genetics* **12**: 825-835.

Ptak, E., and L. R. Schaeffer. 1993. Use of test day yields for genetic evaluation of dairy sires and cows. *Livestock Production Science* **34**: 23-34.

Reents, R., and L. Dopp. 1996. Genetic evaluation for dairy production traits with a test day model for multiple lactations. INTERBULL Open Meeting, Veldhoven, The Netherlands, June 23-24. Pages 113-117 in *Bulletin* **14**. International Bull Evaluation Service, Uppsala, Sweden.

Rekaya, R., M. J. Carabaño**,** and M. A. Toro. 1999. Use of test-day yields for the genetic evaluation of production traits in Holstein-Friesian cattle. *Livestock Production Science* **57**: 203-217.

Schaeffer, L. R., and J.C.M. Dekkers. 1994. Random regressions in animal models for test-day production in dairy cattle. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production.* Guelph, Canada **18**: 443-446.

Schaeffer, L. R., J. Jamrozik, G. J. Kistemaker, and B. J. Van Doormaal. 2000. Experience with a Test-Day Model. *Journal of Dairy Science* **83**: 1135-1144.

Schaeffer, L. R., C. E. Minder, I. McMillan and E. B. Burnside. 1977. Non-linear techniques for predicting 305-day lactation production of Holsteins and Jerseys. *Journal of Diary Science* **60**: 1936-1644.

Sherchand, L., R. W. McNew, D. W. Kellogg and Z. B. Johnson. 1995. Selection of a mathematical model to generate lactation curves using daily milk yields of Holstein cows. *Journal of Dairy Science* **78**: 2507-2513.

Smith, A.F.M., and G. O. Roberts. 1993. Bayesian computation via the Gibbs sampler and related markov chain monte carlo methods. *Journal of Royal Statistical Society B* **55**: 3-24.

Sorensen, D. 1997. *Gibbs sampling in quantitative genetics.* Internal report no82, Danish Institute of Animal Science, Research Centre Foulum, Tjele, Denmark.

Stanton, T. L., L. R. Jones, R. W. Everett, and S. D. Kachman. 1992. Estimating milk, fat, and protein lactation curves with a test day model. *Journal of Diary Science* **75**: 169-1700.

Swalve, H. H. 1995. Test day models in the analysis of dairy production data - a review. *Archiv für Tierzucht* **38**: 11-31.

Swalve, H. H. 2000. Theoretical basis and computational methods for different test-day genetic evaluation models. *Journal of Dairy Science* **83**: 1115-1124.

Van Arendonk, J.A.M., and E. A. Fimland. 1983. Comparison of two methods to extend partial milk records*. Zeitschrift für Tierzucht und Züchtungsbiologie* **100**: 33-38.

Van Arendonk, J.A.M., T. T. Pieters, E.G.H.J. van den Berg, M. H. Pool and A.G.J. Velthuis. 1995. Genetic variation in persistency and its impact on fluctuations in BLUP breeding values for milk production traits. *Journal of Dairy Science* **78** suppl. 1, p293.

Van der Werf, J.H.J. 1990. *Models to estimate genetic parameters in crossbred dairy cattle populations under selection*. Agricultural University Wageningen, Wageningen, The Netherlands, thesis.

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. *Journal of Dairy Science* **81**: 3300-3308.

VanRaden, P. M. 1997. Lactation yields and accuracies computed from test day yields and (co)variancres by best prediction. *Journal of Diary Science* **80**: 3015-3022.

Veerkamp, R. F., and M. E. Goddard. 1998. Covariance functions across herd production levels for test day records on milk, fat and protein yield. *Journal of Dairy Science* **81**: 1690-1701.

Veerkamp, R. F., S. Brotherstone, and T.H.E. Meuwissen. 1999. Survival analysis using random regression models. *Workshop on genetic improvement of functional traits in cattle – longevity – (GIFT)*, Jouy-en-Josas, France.

Veerkamp, R.F., and R. Thompson. 1998. A covariance function for feed intake, liveweigth and milk yield estimated using a random regression model. *Journal of Dairy Science* **82**: 1565-1573.

Wang, C. S, J. J. Rutledge, and D. Gianola. 1994. Bayesian analysis of mixed linear models via Gibbs sampling with an application to litter size in Iberian pigs. *Genetics, Selection and Evolution* **26**: 91-115.

White, I.M.S., and S. Brotherstone. 1997. Modelling lactation curves with cubic splines. 1997. INTERBULL Open Mtg., Vienna, Austria, August 28-29. Pages 80-82 in *Bulletin* **16**. International Bull Evaluation Service, Uppsala, Sweden.

Wiggans, G. R., and M. E. Goddard. 1996. A computationally feasible test day model with separate first and later lactation genetic effects. *Proceedings of the New Zealand Society of Animal Production*. **56**: 19-21.

Wiggans, G. R., and M. E. Goddard. 1997. A computationally feasible test day model for genetic evaluation of yield traits in the United States. *Journal of Dairy Science* **80**: 1795-1800.

Wilmink, J.B.M. 1987a. Adjustment of test-day milk, fat and protein yield for age, season and stage of lactation. *Livestock Production Science* **16**: 335-348.

Wilmink, J.B.M. 1987b. Comparison of different methods of pre-dicting 305-day milk yield using means calculated from within-herd lactation curves. *Livestock Production Science* **17**: 1-17.

Wilmink, J.B.M. 1988. Effects of incomplete records on genetic parameters among cumulative yields in first lactation and on extension of part lactations. *Livestock Production Science* **18**:19-34.

Wood, P.D.P. 1968. Factors affecting the shape of the lactation curve in cattle. *Animal Production* **11**: 307-316.

Woolliams, J. A., and D. Waddington. 1998. The effectiveness of mixed-model smoothing for prediction of lactation yields. *Proceedings of the British Society of Animal Science* 1998 (page 10).

Literatuurlijst

Van Arendonk, J.A.M., T. T. Pieters, E.G.H.J. van den Berg, **M. H. Pool** and A.G.J. Velthuis. 1995. Genetic variation in persistency and its impact on fluctuations in BLUP breeding values for milk production traits. *Journal of Dairy Science* **78**: supplement 1, P293.

Pool M. H. 1996. Genetic trend in female fertility in Dutch dairy cattle. Thesis, Vakgroep Veefokkerij, Wageningen University, The Netherlands.

Pool M. H. 1997. Fokwaardeschatting op basis van individuele proefmelkgegevens "van proefmelkgegevens naar fokwaarden". Veeteelt 1997, december 2.

Oldenbroek J. K., P.A.J. Galesloot, **M. H. Pool** and J.H.J. van der Werf. 1997. Effects of selection for milk yield on feed intake and metabolism of heifers in early lactation. *Proceeding of the European Association for Animal Production 48-th Annual Meeting.* Vienna, Austria, August 25-28. Page 42. Wageningen Pers, Wageningen, The Netherlands.

Pool M. H., T.H.E. Meuwissen. 1997. Prediction of 305-day milk yield from a limited number of test days using a test-day model. INTERBULL Open Meeting, Vienna, Austria, August 28-29. Pages 59-65 in Bull. 16. *International Bull Evaluation Service*, Uppsala, Sweden.

Veerkamp R. F., R. Thompson, T.H.E. Meuwissen, and **M. H. Pool**. 1998. Multi-trait covariance functions to model between animal variation in the dynamic relation between feed intake and milk yield during lactation. Page 69-74 in *Regulation of Feed Intake*, CABI Publishing, CAB international, Wallingford, United Kingdom.

Pool M. H., and T.H.E. Meuwissen. 1999. Prediction of daily milk yields from a limited number of test days using test-day models. *Journal of Dairy Science* **82**:1555-1564

Pool M. H., and T.H.E. Meuwissen. 1999. The effect of incomplete lactation records on covariance function estimates in test-day models. *Proceedings of the European Association for Animal Production 50-th Annual Meeting*, Zurich, Switserland, August 22-26. Page 26. Wageningen Pers, Wageningen, The Netherlands. (H. Wilhelm Schaumann Stiftung scholarship)

Pool M. H., and T.H.E. Meuwissen. 2000. "Reduction of the number of parameters needed for a polynomial random regression test-day model". *Livestock Production Science* **64**: 133-145.

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

Pool M. H., and T.H.E. Meuwissen. 2000. "Stepwise Reducing the Number of Fitted Parameters in Multiple-Trait Lactation Random Regression Test-Day Models". Submitted to *Journal of Dairy Science*. (July, 2000)

Pool M. H., and T.H.E. Meuwissen. 2000. "Reduced rank covariance functions in multi-trait random regression test-day models". *Proceedings of the European Association for Animal Production 51-th Annual Meeting*, Den Hague, The Netherlands, August 21-24. Page 93. Wageningen Pers, Wageningen.

Abbreviations

BLUP	=	Best Linear Unbiased Prediction
cDIM	=	weekly classes of DIM within first and later parities
CF	=	covariance functions
DIM	=	days in milk
EBVs	=	breeding value predictions
LEG	=	Legendre polynomials
MME	=	mixed model
MSEP	=	mean square error of predictions of missing observations
REML	=	Residual Maximum Likelihood estimation
RIP-DIP	=	records in progress dip
RMT	=	reduced rank multi-trait model
RPM	=	repeatability model
RR	=	random regression
RRM	=	random regression model
sDIM	=	standardized days in milk
TDM	=	test-day model

Curriculum Vitae

Op 24 juni 1972 werd ik, Marco Henk Pool, geboren als boerenzoon te Smallingerland (Friesland). In 1989 heb ik het Havo diploma gehaald aan de toenmalige christelijke scholengemeenschap 'het Ichthus college' te Drachten. Na vier jaar studeren aan de Rijks Agrarische Hogeschool (Ahof) te Leeuwarden ben ik in juli 1993 afgestudeerd in de studierichting Nederlandse Landbouw met als specialisatie onderzoek en verdieping veeteelt. In dat zelfde jaar ben ik begonnen met het doorstroomprogramma van de studie Zoötechniek aan de Landbouwuniversiteit te Wageningen. Deze studie heb ik in augustus 1996 afgerond in de oriëntatie veefokkerij, met als keuzevakken informatica. Vanaf april 1996 ben ik als Assistent in Opleiding (AIO) werkzaam geweest binnen de onderzoekschool Wageningen Institute of Animal Science (WIAS) en gedetacheerd bij de afdeling Genetica en Reproductie bij het Instituut voor de Dierhouderij en Diergezondheid (ID-Lelystad) wat onderdeel is van Wageningen University and Reseach Center (WAG-UR). Sinds 1 mei 2000, werk ik in deeltijd als agrarisch consultancy bij de afdeling Genetica en Reproductie van ID-Lelystad BV te Lelystad en hiernaast ben ik in de praktijk werkzaam als agrariër op het ouderlijke melkveebedrijf Pool Wijnjewoude BV in Friesland.

UITNODIGING

Graag wil ik u uitnodigen
voor het bijwonen van de
openbare verdediging van
mijn proefschrift getiteld:

Test-day Models
*Breeding value estimation
based on individual
test-day records*

Op dinsdag 19 december
om 13.30 uur in de Aula van
Wageningen Universiteit,
Generaal Foulkesweg 1a
te Wageningen.

Aansluitend is er een receptie
in café "Vrijheid"
(5 mei plein 13)

Marco Pool
Opperbuorren 3
9241 WL, Wijnjewoude
M.H.Pool@id.wag-ur.nl
Tel. 0650.211.588

Paranimfen:
Piter Bijma, Albert Folkertsma

With compliments

Marco Pool
Institute for Animal Science
and Health (ID-Lelystad)
P.O. Box 65, Lelystad
The Netherlands
email: M.H.Pool@id.wag-ur.nl

Test-day Models
*Breeding value estimation
based on individual
test-day records*

PhD Thesis, WIAS
(Wageningen Institute of
Animal Sciences)

Stellingen

1. Om de genetische parameters in een Test-Dag-Model nauwkeurig te kunnen schatten zijn proefmelkgegevens nodig die de volledige lactatieperiode beschrijven *(dit proefschrift)*.

2. Voor het beschrijven van de lactatiecurve is niet de vorm bepalend maar de onderliggende covariantiestructuur en omdat deze meer complex is, zijn hogere orde functies nodig *(dit proefschrift)*.

3. Biologische functies fitten lactatiecurves slechter dan statistische *(dit proefschrift)*.

4. De toepassing van reactienormen naast random regressie modellen is voor veefokkers: oude wijn in nieuwe zakken.

5. Modellen waarbij tijdsafhankelijke variabelen worden beschreven zijn breed toepasbaar in het onderzoek, maar kosten veel rekentijd en vragen om een gedegen kennis van de statistiek.

6. De razend snelle ontwikkelingen in de computertechnologie maakt dat de wetenschapper over zeer geavanceerde toepassingen beschikt, maar hierin schuilt ook het gevaar dat onderzoeksresultaten morgen al niet meer state-of-the-art zijn.

7. Het bedrijfsleven heeft kennis genoeg om toepassingen uit het onderzoek zelfstandig in de praktijk te testen en besteedt haar geld liever voor onderzoek dat gericht is op het signaleren van kansen voor de wat verdere toekomst.

8. Het grootste probleem van de veehouderij is dat het koopgedrag van de consument verschilt van de publieke opinie. Commerciële bedrijven kijken echter in eerste instantie naar het koopgedrag en pas veel later naar de publieke opinie.

9. Working together: coming together is a beginning, keeping together is progress and working together is success (anoniem)

10. Die Statistiek ist eine grosse Lüge die aus lauter kleinen Wahrheiten besteht. (Lionel Strachey)

11. Kunstmatige intelligentie heeft geen IQ.

12. Geitenhouders moeten geen rozen mee naar huis brengen.

Stellingen bij het proefschrift van Marco H. Pool
'Test-day Models: breeding value estimation based on individual test-day records'
Wageningen, 19 December 2000