Genetics of Parity-Dependant Production Increase and its Relationship with Health, Fertility, Longevity, and Conformation in Swiss Holsteins

T. Neuenschwander,¹ H. N. Kadarmideen,¹ S. Wegmann,² and Y. de Haas¹

¹Statistical Animal Genetics Group, Institute of Animal Sciences, Swiss Federal Institute of Technology, ETH Zentrum CH-8092 Zurich, Switzerland

²Holstein Association of Switzerland, Grangeneuve CH-1725 Posieux, Switzerland

ABSTRACT

Genetic analysis of production increase (ProdI), defined as an increase in production from early to later lactations, was conducted using data from the Holstein Association of Switzerland. This production increase describes the maturity rate of the cow. The data set contained 42,807 cows with a ProdI value. All cows had completed the first 3 lactations. Different formulas were derived for the computation of ProdI using 1) milk yields or energy-corrected milk yields and 2) yields from all 3 lactations or only 2 of them (first and second, first and third, second and third). Heritabilities of ProdI and genetic and phenotypic correlations of ProdI with somatic cell score, days to first service, nonreturn rate, longevity, and 27 conformation traits were estimated by univariate and bivariate sire models that included relationship among sires. Heritabilities for ProdI were low (0.06 to 0.08), but genetic variation among sires existed. For nonreturn rate and longevity, regressions on the sire estimated breeding values were estimated. Additive genetic correlations of ProdI were moderately favorable with somatic cell score (–0.22 to –0.33) and chest width (0.21 to 0.30), i.e., with traits often associated with long-lasting cows. Unfavorable correlations were found with angularity (–0.18 to –0.26). Regression coefficients from regressing ProdI on sire estimated breeding values for longevity tend to show favorable relationships between these 2 traits (0.10 to 0.20). Results show that animals can be selected for ProdI, as there is good genetic variation between bulls. ProdI is a potential trait to be included in selection indices, as it has favorable genetic relationships with economically important functional traits such as health, conformation, and longevity.

(Key words: production increase, maturity rate, functional trait, conformation)

Abbreviation key: DFS = days to first service, ECM = energy-corrected milk, ECMI = production increase for energy-corrected milk, ECMI_{ij} = production increase for energy-corrected milk from lactation i to j, ID = identification number, MilkI = production increase for milk, MilkI_{ij} = production increase for milk from lactation i to j, NRR = nonreturn rate, ProdI = production increase.

INTRODUCTION

Toward the end of the 20th century, the dairy cow (particularly the Holstein cow) has had difficulties maintaining a long productive life. During the 1980s and part of the 1990s, selection was focused almost entirely on protein production (e.g., INET in the Netherlands; Van der Beek, 1999) and, in a few countries, also on conformation (e.g., LPI in Canada; Boettcher and Van Doormaal, 1999). A huge increase in production per lactation was the result. However, the ability of Holstein cows to survive in their environment decreased (Uribe et al., 1995; Rupp and Boichard, 1999). In search of a remedy, a new set of traits, called “functional traits,” were recorded and selected for. These traits are defined as the characteristics of an animal that increase their efficiency through reduced input costs, rather than higher output of products (Groen et al., 1998a). The most common functional traits are mastitis resistance, resistance to lameness, fertility, calving ease, and longevity. All or some of these functional traits now enter into breeding goals and selection indices of the dairy breeds.

Based on results of the conformation evaluation, adulthood of a dairy cow can be assumed to be reached at 60 mo of age (S. Wegmann, personal communication, 2004), but cows first calve at a much younger age. Depending on the housing conditions (varying from intensive rearing to extensive alpine pasture conditions in Switzerland), age at first calving varies between 18 and 36 mo. Therefore, most of the milking heifers are still growing during their first lactation and part of the energy and protein intake will be assigned to this purpose (Veerkamp, 2000). Milk production of most dairy cows

Received August 26, 2004.

Accepted November 11, 2004.

Corresponding author: Y. de Haas; e-mail: Yvette.deHaas@inw.agrl.ethz.ch.

will increase from first to second and from second to third lactation as the cow grows close to mature size and is able to use more nutrients for milk production. However, the amount of increase is different among cows. There is genetic variance for maturity rate (Krogmeier et al., 2003), i.e., some animals have a genetic predisposition to produce moderately in first lactation and to increase production levels in second and third lactations.

Some breeders try to breed cows with moderate first lactation production and high yields in subsequent lactations so as to reach the full production potential at 60 mo of age. In breeders' circles, this gradual production increase (**ProdI**), a measure of the maturity rate, is believed to be found in trouble-free cows. Geneticists became interested in this new trait and tried to define it in a way that would enable selection. Two definitions have been proposed: 1) the definition used in Switzerland, based on the EBV for each of the first 3 lactations (Schleppi and Bigler, 2002) and 2) the use of real lactation yields of the cows instead of EBV (Krogmeier et al., 2003). However, no study has estimated genetic parameters for ProdI computed with actual lactation records. The hypothesis of possible links of ProdI with functional traits at a genetic or phenotypic level has never been investigated. Because health and fertility are important components of productive life (Pryce and Brotherstone, 1999), it is worthwhile to estimate genetic and phenotypic correlations of ProdI with these functional traits.

The objectives of this study were 1) to investigate the formula used to estimate ProdI, using the real lactation yields, and to find possibilities of improving it; 2) to estimate the variance components of ProdI; and 3) to quantify genetic and phenotypic correlations between ProdI and udder health, longevity, fertility, and conformation.

MATERIALS AND METHODS

Available Data

Records were available from the Holstein Association of Switzerland for production traits, SCC, inseminations, and conformation. Sire EBV for longevity and non-return rate (**NRR**) were also available, as well as the pedigree of all animals.

Thirteen years of production records with calving dates from 1991 through 2004 were in the production data set. This data set consisted of all lactations with at least one test-day, resulting in 221,850 cows with 551,784 lactations. The data set contained the cow identification number (**ID**); parity; herd ID; date of calving; milk, fat, and protein yields in 305-d and in total lactation; DIM; and status of the lactation (i.e., completed

or not). Records of SCC were given as test-day results, recorded since 1994. In total 1,172,244 insemination records were available from 1994 to 2004. Conformation data, recorded since 1991 in Switzerland, included 21 linear traits, 5 composites, and final score for 140,325 cows. Linear traits were measured on a scale of 1 to 9; for first lactation heifers, composites were on a scale from 50 to 87; for dairy character, the scale went up to 90.

The pedigree file contained ID of the animal and of its sire and dam. Number of bulls and cows in the pedigree file were 153,011 and 589,225, respectively. Pedigrees were traced as far back as 1940 for the bulls and 1942 for the cows.

Trait Definitions and Data Editing

A data set containing ProdI, SCS, days to first service (**DFS**), NRR, longevity, and conformation was constructed with the available data.

ProdI was calculated as follows:

$$\text{ProdI} = \frac{(2 \times M_2) + (3 \times M_3)}{5} - M_1 \quad [1]$$

where M_x is the milk yield or energy-corrected milk (**ECM**) yield in lactation x , $x = 1, 2$ or 3 . The ProdI for milk yield was defined as **MilkI** and, for ECM yield, was defined as **ECMI**. This formula is adapted from Schleppi and Bigler (2002). For milk yield, standard 305-d lactation yields were used, which consisted of cows with at least 270 DIM with lactation recorded as "ended." The standard 305-d milk yields meant that lactations with 270 to 304 DIM were multiplied by a correction factor used by the Holstein Association of Switzerland (Wegmann, 2004, personal communication).

The ECM was computed with the following equation:

$$\text{ECM} = c \times M \times \frac{0.37\text{Fd} + 0.21\text{Pd} + 0.95}{3.1} \quad [2]$$

where c is the correction factor for lactations with <305 d, M is the milk yield, Fd is the fat deviation, and Pd is the protein deviation (Kirchgeßner, 1997). The following restrictions were applied to exclude outliers: milk and ECM yield had to be between 2000 and 16,000 kg, age at first calving had to be at least 500 d and <2500 d for third calving.

In a later analysis, the ProdI formula was reconstructed to try to improve its accuracy in describing the increase of production. The difference between the first and second lactation, respectively, was defined as **MilkI12** and **ECMI12**; the difference between the first

and third lactation was defined as **MilkI13** and **ECMI13**, respectively; and, finally, the difference between the second and third lactation, respectively, was defined as **MilkI23** and **ECMI23**. These ProdI formulas aim to assess the increase of production in a more detailed way.

Lactation SCS was computed using test-day SCC data and was used for the variance component estimates. Test-day SCS was calculated as

$$\text{SCS} = \left(\log_2 \frac{\text{SCC}}{100,000} \right) + 3. \quad [3]$$

Lactation SCS was computed as the average of test-day SCS within lactations (i.e., made up to the 305th d of the lactation). The use of lactation SCS instead of SCC is based on the linearity of SCS (Ali and Shook, 1980) and has been used to analyze test-day SCC in many studies (Mrode and Swanson, 1996; de Haas et al., 2002). For this data set, plausibility restrictions were set at 0 and 8 for lactation SCS.

The first trait used for fertility was DFS and was computed as the interval between calving and first recorded insemination (in days). Plausibility values were set at 20 d as the lower limit and 180 d as the upper limit to avoid possible biases from cows that were physiologically abnormal or incorrect recording of calving or insemination dates. Days to first service after each of the first 3 calvings were computed. The second fertility trait used, NRR, is defined in Switzerland as a binary trait recording the absence or presence of insemination during the 56 d following the first insemination. The EBV of the sires were used for the evaluations with NRR to avoid the problem related to the analysis of binary traits. The NRR EBV are estimated by the Holstein Association with an animal model (Schnyder and Stricker, 2002).

The EBV of sires for their daughters' longevity were used in calculating relationship between ProdI and longevity. In Switzerland, longevity is defined as the productive life, which is the life span between first calving and the last test date on official milk recording. Longevity EBV are estimated with a sire-maternal grandsire survival model (Vukasinovic et al., 2001).

Conformation analyses were made with classification results of first lactation heifers. Age at first calving had to be <1250 d, and the classification had to be made within 1 yr after calving.

The data were edited in a stepwise manner. First, only lactations 1 to 3 of the production data set were kept. Only cows with records in all 3 lactations and with known sires were taken for further analysis. Records on other traits (SCS, DFS, and conformation) were added when available (i.e., not all cows had records on all

Table 1. Number of animals in the dataset with records for production increase (ProdI), for SCS and days to first service (DFS) in each of the first 3 lactations, and for conformation.

	Quantity
Cows with ProdI	42,807
ProdI + SCS ¹	28,840
ProdI + SCS2	29,879
ProdI + SCS3	29,915
ProdI + DFS ¹	30,410
ProdI + DFS2	35,062
ProdI + DFS3	38,380
ProdI + conformation	28,250

¹SCSi = SCS, where i = lactation 1 to 3.

²DFSi = DFS, where i = lactation 1 to 3.

other traits). Final editing was done by excluding daughters of bulls with <6 daughters and cows in herds with <6 cows. This resulted in a data set of 42,807 cows with an observation for ProdI. Number of cows with records for other traits is shown in Table 1. Calving dates of these cows were between January 1991 and July 2003.

Pedigree was reconstituted to 4 generations back and contained 800 bulls. The oldest bull in the pedigree was born in 1942.

Statistical Models and Analyses

Variance components were estimated with sire models. Considering the number of traits for which the correlation had to be computed, sire model was preferred over animal model for the genetic analyses.

The univariate sire model used was as follows:

$$y = \mu + \text{fixed effects} + s + e \quad [4]$$

where y is the observation, μ is the overall mean, s is the random effect of the sire, and e is the residual. Fixed effects differed from trait to trait. The use of each one of them is summarized in Table 2. The program ASREML (Gilmour et al., 2001) was used for estimation of all variance components and regression coefficients. This software estimates variance components by REML.

The sire effects were linked through the relationship matrix built using the pedigree file. They were assumed to be normally distributed. Fixed effects were 1) herd of calving for each of the 3 lactations [with 2357 herds of first lactation (Herd1), 2381 herds of second lactation (Herd2), and 2391 herds of third lactation (Herd3); 4.7 and 7.5% of cows changed herd between first and second lactation and first and third lactation, respectively]; 2) an interaction between year and season of each calving [two seasons were defined, March to August and September to February; 22 yr-season classes of first lacta-

Table 2. Fixed effects (f) and covariates (c) used in the model.

Trait	ProdI ¹	SCS1 ²	SCS2	SCS3	DFS1 ³	DFS2	DFS3	Conf ⁴
μ	f	f	f	f	f	f	f	f
Herd1 ⁵	f	f			f			f
Herd2	f		f			f		
Herd3	f			f			f	
YS1 ⁶	f	f			f			f
YS2	f		f			f		
YS3	f			f			f	
Age1 ⁷	c	c			c			c
Age2	c		c			c		
Age3	c			c			c	
DIM1 ⁸	c	c			c			c
DIM2	c		c			c		
DIM3	c			c			c	
Classifier								f
DTC ⁹								c

¹ProdI = Production increase.²SCSi = SCS, where i = lactation 1 to 3.³DFSi = Days to first service, where i = lactation 1 to 3.⁴Conf = Conformation traits.⁵Herd_i = Herd of the cow, where i = lactation 1 to 3.⁶YS_i = Year-season of calving, where i = lactation 1 to 3.⁷Age_i = Age at calving, where i = lactation 1 to 3.⁸DIM_i = DIM, where i = lactation 1 to 3.⁹DTC = Days between calving and classification.

tion (YS1) were defined, 23 yr-season classes of second lactation were defined (YS2), and 23 yr-season classes of third lactation were defined (YS3)]; 3) age at each calving as a covariate; 4) DIM for each lactation as a covariate; 5) classifier (16 classifiers); and 6) days from first calving to classification as a covariate.

Because ProdI has information from all 3 lactations, all fixed effects related to production were used. The other traits had only those fixed effects related to the corresponding lactation. Moreover, classification effects (classifier and time to classification) were included as fixed effects for analyses of conformation traits. Bivariate sire model analyses were conducted to estimate the (co)variances and correlations between ProdI and the other traits. Genetic and phenotypic parameters were computed based on the estimated variance components.

Regressions (*b*) of daughter ProdI records on their sire EBV for longevity and NRR were estimated by a univariate analysis. The model was

$$y = \mu + \text{fixed effects} + \text{EBV}_x + e \quad [5]$$

where EBV_x is a sire EBV of trait *x* (longevity or NRR), fitted as a covariate, and all other terms are as described previously under equation [4].

RESULTS

Maturity Rate

Descriptive statistics as well as heritability estimates and their standard errors are presented in Table 3.

The mean of MilkI is 1234 kg and 1268 kg for ECMI. Production increased also from lactation 2 to 3, but had a higher coefficient of variation (SD_p/μ) than the 2 others (163% for MilkI23 compared with 85 and 61% for MilkI12 and MilkI13, respectively). Heritability estimates were low for all ProdI (between 0.01 and 0.08) but especially for MilkI23 and ECMI23, which had a heritability that was not significantly different from zero. Effect of age on standard MilkI and ECMI was negative for first and second lactation and positive for third lactation. A similar pattern was found for DIM.

The distribution of the sires PTA of MilkI is shown in Figure 1. Only bulls with >50 daughters were included to avoid low reliability, giving a total of 148 bulls plotted. The distribution of the sire PTA for MilkI shows a normal distribution; 64% of the bulls have a PTA between -80 and 80. Though MilkI has a low heritability, there is variance among the sire PTA.

Functional Traits

Average of SCS was 2.48, but the mean SCS increased with parity (from 2.13 to 2.81). Mean DFS was 81 d over all 3 lactations and did not show a trend linked with parity. Heritability of DFS was low (0.03). Conformation trait means ranged from 4.40 (pasterns) to 6.19 (rear teat placement). Phenotypic standard deviation (σ_p) ranged from 0.73 to 1.67. The heritability estimates were between 0.10 (heel depth) and 0.49 (stature). Composites had heritabilities between 0.14 (feet and legs)

Table 3. Descriptive statistics of production increase traits, udder health traits, fertility traits, and conformation with mean, additive genetic (SD_a), and phenotypic (SD_p) standard deviation.

Trait	Unit	Mean	SD_a	SD_p	h^2	SE
MilkI ¹	kg	1234.00	216.05	736.47	0.08	0.01
ECMI ²	kg	1268.00	205.43	718.38	0.08	0.01
MilkI12 ³	kg	920.00	204.60	783.74	0.07	0.01
MilkI13	kg	1444.00	234.60	886.47	0.07	0.01
MilkI23	kg	523.60	103.68	853.56	0.01	0.00
ECMI12 ⁴	kg	968.50	179.65	750.79	0.06	0.01
ECMI13	kg	1468.00	227.51	870.06	0.07	0.01
ECMI23	kg	499.90	97.93	825.50	0.01	0.00
SCS1 ⁵	score	2.13	0.44	1.00	0.18	0.02
SCS2	score	2.49	0.47	1.05	0.19	0.02
SCS3	score	2.81	0.46	1.11	0.17	0.02
DFS1 ⁶	d	80.70	4.48	25.30	0.03	0.01
DFS2	d	79.90	4.62	24.99	0.03	0.01
DFS3	d	81.36	4.63	26.14	0.03	0.01
Final score	score	78.35	1.07	1.70	0.36	0.03
Frame/capacity	score	77.69	2.69	4.00	0.41	0.04
Rump	score	79.04	2.17	3.70	0.32	0.03
Dairy character	score	79.46	1.55	2.64	0.32	0.03
Feet and legs	score	78.18	1.11	2.98	0.14	0.02
Mammary system	score	78.72	1.15	2.27	0.24	0.03
Stature	score	5.45	1.00	1.35	0.49	0.04
Heart girth	score	5.57	1.06	1.67	0.37	0.03
Chest width	score	5.11	0.57	1.11	0.25	0.03
Body depth	score	5.91	0.56	0.89	0.36	0.03
Loin	score	5.76	0.51	0.93	0.28	0.03
Rump angle	score	4.42	0.52	0.89	0.32	0.03
Pin width	score	5.89	0.75	1.07	0.44	0.04
Angularity	score	5.59	0.40	0.73	0.28	0.03
Rear legs side view	score	5.72	0.30	0.74	0.16	0.02
Pasterns	score	4.40	0.31	0.77	0.16	0.02
Heel depth	score	4.83	0.27	0.83	0.10	0.02
Rear legs rear view	score	5.30	0.32	0.91	0.12	0.02
Fore attachment	score	5.24	0.52	1.05	0.23	0.03
Rear attachment height	score	4.79	0.64	1.17	0.28	0.03
Rear attachment width	score	5.33	0.43	0.92	0.21	0.02
Median suspensory	score	5.76	0.49	0.99	0.23	0.02
Udder depth	score	5.14	0.60	1.09	0.29	0.03
Udder texture	score	5.60	0.51	0.91	0.29	0.03
Teat length	score	4.76	0.52	0.91	0.30	0.03
Front teat placement	score	4.54	0.61	0.95	0.38	0.03
Rear teat placement	score	6.19	0.51	0.91	0.29	0.03

¹MilkI = Production increase for milk = $((2 \times M_2) + (3 \times M_3))/5 - M_1$, where M_x is the milk yield in lactation x , $x = 1, 2$, or 3 .

²ECMI = Production increase for ECM = $((2 \times ECM_2) + (3 \times ECM_3))/5 - ECM_1$, where ECM_x is the ECM yield in lactation x , $x = 1, 2$, or 3 .

³MilkI_{ij} = Maturity rate for milk between lactation i and j = milk yield _{j} – milk yield _{i} .

⁴ECMI_{ij} = Maturity rate for ECM between lactation i and j = ECM yield _{j} – ECM yield _{i} .

⁵SCSi = SCS, where i = lactation 1 to 3.

⁶DFS _{i} = Days to first service, where i = lactation 1 to 3.

and 0.41 (frame/capacity). Final score had a mean of 78.35 and a heritability of 0.36. Standard errors for all functional traits were <0.05.

Correlation of Prodl with Functional Traits

Additive genetic and phenotypic correlations between MilkI and SCS, DFS, and conformation traits are presented in Table 4. Each of the 3 lactations shows favorable additive genetic correlations between SCS and MilkI (–0.30, –0.30, and –0.29). Some rump traits [loin

(–0.19) and pin width (–0.20)] have significant negative genetic correlations with MilkI. Chest width (0.30) and heart girth (0.24) have moderate positive genetic correlations with MilkI. Phenotypic correlations were generally small but in the same direction as genetic correlations and had high standard errors.

Correlations between ECMI and the other traits were generally smaller than those between MilkI and these traits (Table 5).

Additive genetic correlations computed with MilkI12 and MilkI13 were quite similar to those computed with

Figure 1. Distribution for PTA of production increase of kilograms of milk (ProdI Milk) of bulls with at least 50 daughters.

MilkI (Table 6). However, estimates with MilkI23 seem to be different. The latter trait also had high standard errors (0.13 to 0.19). The MilkI12 had a moderately unfavorable correlation with rear attachment width. The MilkI13 was negatively correlated with loin and angularity. The MilkI23 had a moderately negative correlation with DFS in third lactation, but low correlations with SCS. Similar results are found for ECMI (Table 7).

Estimated regression coefficients of MilkI and ECMI on longevity and NRR are given in Table 8. Regression was positive and significant for longevity and negative for NRR, but generally not significant.

DISCUSSION

This study has as its main objective, the estimation of genetic and phenotypic parameters for ProdI, including its correlations with SCS, DFS, NRR, longevity, and conformation. This objective can be summed up in 3 questions: 1) what is the optimal definition of ProdI, 2) how is ProdI correlated to the other functional traits, and 3) is there an advantage of breeding for ProdI in addition to production yields.

ProdI Definitions

Evaluation of the standard ProdI formula was made with 3 changes on the formula of Schleppi and Bigler (2002). These were 1) the use of actual production yields instead of EBV to avoid the correlations used in the multivariate estimations of test-day EBV, 2) the absence of correction factors used to account for the differences in standard deviations in each lactation (because it was not used by the Holstein Association of Switzerland) (Wegmann, 2004, personal communication), and 3) the replacement of fat and protein yields by milk (MilkI) or ECM (ECMI) yields. The latter change was

Table 4. Additive genetic (r_g) and phenotypic (r_p) correlations between production increase for milk (MilkI¹) and different functional traits.

Trait	r_g	SE_g	r_p	SE_p
SCS1 ²	-0.30†	0.09	0.01	0.01
SCS2	-0.30†	0.09	-0.12	0.01
SCS3	-0.29†	0.09	-0.16	0.01
DFS1 ³	-0.08	0.14	-0.03	0.01
DFS2	0.12	0.12	0.03	0.01
DFS3	0.02	0.12	0.00	0.01
Final score	0.06	0.09	-0.04	0.01
Frame/capacity	0.09	0.09	-0.03	0.01
Rump	-0.09	0.08	-0.04	0.01
Dairy character	-0.17	0.09	-0.09	0.01
Feet and legs	0.06	0.10	-0.01	0.01
Mammary system	0.08	0.09	0.00	0.01
Stature	-0.05	0.08	-0.03	0.01
Heart girth	0.24†	0.08	-0.02	0.01
Chest width	0.30†	0.09	-0.01	0.01
Body depth	0.01	0.09	-0.06	0.01
Loin	-0.19†	0.09	-0.05	0.01
Rump angle	-0.13	0.09	-0.02	0.01
Pin width	-0.20†	0.08	-0.04	0.01
Angularity	-0.24†	0.08	-0.09	0.01
Rear leg side view	0.11	0.10	0.01	0.01
Pasterns	-0.07	0.10	-0.01	0.01
Heel depth	0.18	0.10	0.00	0.01
Rear leg rear view	0.12	0.10	-0.03	0.01
Fore attachment	-0.03	0.09	0.05	0.01
Rear attachment height	0.17	0.09	0.02	0.01
Rear attachment width	-0.16	0.09	-0.09	0.01
Median suspensory	-0.01	0.09	0.00	0.01
Udder depth	0.11	0.09	0.15	0.01
Udder texture	-0.02	0.09	-0.05	0.01
Teat length	0.19†	0.09	0.02	0.01
Front teat placement	0.01	0.09	-0.01	0.01
Rear teat placement	-0.03	0.09	-0.02	0.01

¹MilkI = Production increase for milk = $((2 \times M_2) + (3 \times M_3))/5 - M_1$, where M_x is the milk yield in lactation x , $x = 1, 2$, or 3 .

²SCSi = SCS, where i = lactation 1 to 3.

³DFSi = Days to first service, where i = lactation 1 to 3.

†Genetic correlations were significantly different from zero.

made to evaluate maturity rate as a functional trait: milk is a measure of the amount of fluid put in the udder of the heifer and, therefore, describes the constraints put on the udder during its early development. Energy-corrected milk is a measure of the energy content of milk and is, therefore, an indicator of the energy needed for milk production that cannot be used for growth; for the same reason, it is also a measure of the metabolic stress of the cow. Fat and protein production, which is currently used in Swiss breeding schemes, would have described these effects less accurately.

Later on, a second group of ProdI formulas was made to define more precisely the increase between each of the lactations. The formula of Schleppi and Bigler (2002) showed the global increase of the production from the first to the third lactations, but the increase between any 2 of them was not described. The standard ProdI does not reveal whether the increase was made

Table 5. Additive genetic (r_g) and phenotypic (r_p) correlations between production increase for energy-corrected milk (ECMI¹) and different functional traits.

Trait	r_g	SE _g	r_p	SE _p
SCS1 ²	-0.25†	0.10	0.01	0.01
SCS2	-0.29†	0.09	-0.12	0.01
SCS3	-0.30†	0.09	-0.15	0.01
DFS1 ³	-0.13	0.14	-0.03	0.01
DFS2	0.01	0.13	0.02	0.01
DFS3	-0.08	0.13	0.00	0.01
Final score	0.03	0.09	-0.04	0.01
Frame/capacity	0.07	0.09	-0.04	0.01
Rump	-0.10	0.09	-0.04	0.01
Dairy character	-0.17	0.09	-0.07	0.01
Feet and legs	0.04	0.10	-0.02	0.01
Mammary system	0.07	0.09	0.00	0.01
Stature	-0.08	0.09	-0.04	0.01
Heart girth	0.18†	0.09	-0.04	0.01
Chest width	0.24†	0.09	-0.03	0.01
Body depth	0.00	0.09	-0.06	0.01
Loin	-0.16	0.09	-0.04	0.01
Rump angle	-0.17	0.09	-0.03	0.01
Pin width	-0.12	0.08	-0.04	0.01
Angularity	-0.23†	0.09	-0.07	0.01
Rear legs side view	0.13	0.10	0.02	0.01
Pasterns	-0.03	0.10	-0.01	0.01
Heel depth	0.22	0.10	0.00	0.01
Rear legs rear view	0.03	0.10	-0.05	0.01
Fore attachment	-0.04	0.09	0.05	0.01
Rear attachment height	0.12	0.09	0.01	0.01
Rear attachment width	-0.19	0.09	-0.10	0.01
Median suspensory	-0.01	0.09	0.01	0.01
Udder depth	0.14	0.09	0.15	0.01
Udder texture	-0.05	0.09	-0.04	0.01
Teat length	0.18	0.09	0.01	0.01
Front teat placement	-0.03	0.09	-0.01	0.01
Rear teat placement	-0.02	0.09	-0.01	0.01

¹ECMI = Production increase for ECM = $((2 \times \text{ECM}_2) + (3 \times \text{ECM}_3)) / 5 - \text{ECM}_1$, where ECM_x is the ECM yield in lactation x , $x = 1, 2$, or 3.

²SCSi = SCS, where i = lactation 1 to 3.

³DFSi = Days to first service, where i = lactation 1 to 3.

†Genetic correlations were significantly different from zero.

at the second lactation, at the third lactation, or at both. The second group of formulas allowed the evaluation of each increase, i.e., between first and second lactation, first and third lactation, and second and third lactation. The similarities of variance components between the 3 ProdI in which first lactation was the base of comparison (MilkI12, MilkI13, and standard MilkI) show the importance of this lactation for maturity rate. Increases from first lactation to second, third, or both have the same patterns. For maturity rate, the emphasis must be put on what was produced in first lactation compared with any of the subsequent lactations. The MilkI23 and ECMI23 seemed to be different in both means and variances to standard MilkI and ECMI. The large coefficient of variation found for MilkI23 and ECMI23 shows that the increase in production for this trait has a high error, and, therefore, the increase is not as important as in

ProdI, including first lactation. Moreover, MilkI23 and ECMI23 had heritabilities that were not different from zero, which resulted in high standard errors for all correlations estimated between these traits and other functional traits. For the latter reason, MilkI23 and ECMI23 will not be discussed any further.

Heritability estimates of the other ProdI were in the range of functional traits, not unlike udder health, fertility, and resistance to disease (Uribe et al., 1995; Kardamdeen et al., 2000; VanRaden et al., 2004). All ECMI showed higher means than MilkI. Therefore, a limiting factor for production in first lactation is energy needs (ECM) rather than udder capacity (milk). A cow with enough energy resources will produce the amount of milk related to it. Udder capacity will only play a minor role for the limitation of milk production. Therefore, it is good to breed for tight udders (i.e., high udder depth), as milk production will not be hindered much. Moreover, tight udders are positively correlated with longevity (Pasman and Reinhardt, 1999).

Correlations between MilkI and first lactation yield were computed to see whether there was a bias in the data set caused by the use of cows with at least 3 lactations ended. Cows culled in the first lactation because of poor milk production or on the contrary because of problems caused by a high first lactation milk yield could have biased the results. There is a slightly negative genetic correlation (-0.23), but the standard error is relatively high (0.08). Therefore, we may assume that the bias caused by daughters culled during their first lactation is not big enough to have an impact on the analyses.

Correlations Between ProdI and Some Functional Traits

Genetic and phenotypic correlations were estimated between ProdI and SCS, DFS, NRR, longevity, and conformation. All ProdI have similar genetic correlation estimates with these traits. Therefore, to avoid redundancy, only the results of one ProdI (ECMI13) will be given, and when differences occur, they will be mentioned.

Udder health. Somatic cell score was used as an indicator of udder health. Genetic correlations between lactation SCS and occurrence of clinical mastitis during the same lactation were medium to high (0.7) as reviewed by Mrode and Swanson (1996). Lund et al. (1994) reported a high estimate of 0.97 between SCS and clinical mastitis. The mean SCS of the current study (2.48) is in the same range as those estimated by de Haas et al. (2002). Weller et al. (1992) found a lower increase in SCS from first to third parity (2.00 to 2.28)

Table 6. Correlations between production increase for milk between first and second lactation, first and third lactation, second and third lactation (MilkIij),¹ and functional traits.

Trait	MilkI12 ²		MilkI13 ³		MilkI23 ⁴	
	r _g	r _p	r _g	r _p	r _g	r _p
SCS1 ⁵	-0.30†	0.02	-0.23†	0.01	-0.10	0.00
SCS2	-0.30†	-0.15	-0.22†	-0.06	0.03	0.07
SCS3	-0.30†	-0.07	-0.27†	-0.17	-0.11	-0.12
DFS1 ⁶	0.03	-0.02	-0.15	-0.03	-0.33	-0.01
DFS2	0.23	0.03	0.05	0.02	-0.31	-0.01
DFS3	0.15	-0.01	-0.04	0.01	-0.38†	0.03
Final score	0.06	-0.03	0.06	-0.04	-0.09	-0.01
Frame/capacity	0.13	-0.02	0.07	-0.03	-0.13	-0.02
Rump	-0.08	-0.04	-0.09	-0.03	-0.05	0.00
Dairy character	-0.11	-0.07	-0.18	-0.08	-0.22	-0.01
Feet and legs	0.09	-0.01	0.04	-0.01	-0.17	0.00
Mammary system	0.04	0.00	0.11	0.00	0.08	0.00
Stature	0.00	-0.02	-0.07	-0.03	-0.18	-0.01
Heart girth	0.25†	-0.01	0.22†	-0.02	0.01	-0.01
Chest width	0.30†	0.00	0.29†	-0.02	0.05	-0.01
Body depth	0.03	-0.05	0.00	-0.06	-0.07	-0.02
Loin	-0.13	-0.04	-0.21†	-0.04	-0.18	-0.01
Rump angle	-0.09	-0.02	-0.14	-0.02	-0.09	0.00
Pin width	-0.20†	-0.04	-0.18†	-0.04	-0.06	-0.01
Angularity	-0.18	-0.08	-0.26†	-0.08	-0.27	-0.01
Rear leg side view	0.01	0.01	0.15	0.01	0.32†	0.00
Pasterns	-0.01	-0.01	-0.10	0.00	-0.19	0.00
Heel depth	0.12	0.00	0.17	0.00	0.06	0.00
Rear leg rear view	0.09	-0.03	0.12	-0.03	0.00	0.00
Fore attachment	-0.02	0.05	-0.04	0.04	-0.09	-0.01
Rear attachment height	0.20	0.02	0.16	0.01	-0.05	0.00
Rear attachment width	-0.14†	-0.08	-0.16	-0.08	-0.13	-0.01
Median suspensory	-0.06	-0.01	0.02	0.01	0.17	0.02
Udder depth	0.09	0.13	0.12	0.13	0.06	0.02
Udder texture	0.02	-0.04	-0.03	-0.04	-0.05	0.00
Teat length	0.18	0.02	0.19†	0.02	0.12	0.00
Front teat placement	-0.01	0.00	0.02	-0.02	-0.01	-0.01
Rear teat placement	-0.04	-0.02	-0.02	-0.01	0.05	0.00

¹MilkIij = Maturity rate for milk between lactation i and j = milk yield_j – milk yield_i.

²Standard errors of r_g were between 0.08 and 0.14; SE of r_p were all 0.01.

³Standard errors of r_g were between 0.08 and 0.14; SE of r_p were all 0.01.

⁴Standard errors of r_g were between 0.13 and 0.18; SE of r_p were all 0.01.

⁵SCSi = SCS, where i = lactation 1 to 3.

⁶DFSi = Days to first service, where i = lactation 1 to 3.

†Genetic correlations were significantly different from zero.

than in the present study. Heritability of SCS (0.17 to 0.19) is high for this trait: Mrode and Swanson (1996) reported average heritability estimates of 0.11 for each of the first 3 lactations based on a review of studies. Weller et al. (1992) observed a heritability estimate of 0.19 for first lactation SCS, similar to the present study. The genetic correlation of ECMI with SCS in third parity is larger than with SCS in first parity. The amount of milk produced during the first lactation has an unfavorable effect on udder health in the same lactation (Kadarmideen et al., 2000), but, based on the correlations computed between ProdI and the different SCS, it has a stronger negative effect on SCS in later lactations. High milk production in the first lactation reduces the action of the immune system in the udder and leads to damage that will last for the subsequent lactations

(Rupp et al., 2000). A moderate first lactation production, compared with adult production, is part of having a healthy udder; it allows enough protection of the udder and, therefore, allows time for it to develop into a full producing mammary system. Another understanding of the correlation between SCS and maturity rate would be that the damage to the udder by a case of clinical mastitis in first lactation hinders a high production increase in the following lactations.

Average additive genetic correlations between ProdI and SCS of the first 3 lactations (–0.29) are slightly larger than those computed by Krogmeier et al. (2003), who worked with Fleckvieh (dual-purpose German Simmental) and Brown Swiss breeds (–0.20 and –0.25, respectively). One of the reasons for the smaller values found by Krogmeier et al. (2003) could be a consequence

Table 7. Additive genetic (r_g) and phenotypic (r_p) correlations between production increase for energy-corrected milk (ECM) between first and second lactation, first and third lactation, second and third lactation (ECMI $_{ij}$),¹ and functional traits.

Trait	ECMI12 ²		ECMI13 ³		ECMI23 ⁴	
	r_g	r_p	r_g	r_p	r_g	r_p
SCS1 ⁵	-0.32†	0.00	-0.26†	0.00	-0.04	0.00
SCS2	-0.33†	-0.15	-0.31†	-0.07	-0.08	0.07
SCS3	-0.32†	-0.06	-0.30†	-0.16	-0.09	-0.12
DFS1 ⁶	-0.03	-0.02	-0.17	-0.03	-0.33	-0.01
DFS2	0.14	0.03	-0.06	0.01	-0.40†	-0.01
DFS3	0.04	-0.01	-0.13	0.01	-0.41†	0.02
Final score	0.07	-0.03	0.02	-0.04	-0.17	-0.01
Frame/capacity	0.14	-0.03	0.03	-0.04	-0.22	-0.02
Rump	-0.10	-0.04	-0.10	-0.03	-0.09	0.00
Dairy character	-0.12	-0.06	-0.17	-0.06	-0.16	0.00
Feet and legs	0.06	-0.02	0.03	-0.02	-0.14	0.00
Mammary system	0.07	0.00	0.08	0.01	0.01	0.00
Stature	-0.01	-0.02	-0.11	-0.03	-0.25	-0.01
Heart girth	0.22†	-0.02	0.15†	-0.04	-0.09	-0.02
Chest width	0.28†	-0.02	0.21†	-0.04	-0.07	-0.02
Body depth	0.03	-0.05	-0.02	-0.06	-0.10	-0.02
Loin	-0.13	-0.03	-0.16	-0.03	-0.14	0.00
Rump angle	-0.12	-0.02	-0.18†	-0.02	-0.16	0.00
Pin width	-0.13	-0.03	-0.11	-0.03	-0.08	-0.01
Angularity	-0.18	-0.06	-0.24†	-0.06	-0.21	0.00
Rear leg side view	0.04	0.01	0.16	0.01	0.28	0.00
Pasterns	0.05	0.00	-0.07	-0.01	-0.23	0.00
Heel depth	0.14	0.00	0.21	0.00	0.09	0.00
Rear leg rear view	0.01	-0.04	0.03	-0.04	-0.05	-0.01
Fore attachment	0.00	0.05	-0.06	0.04	-0.13	-0.01
Rear attachment height	0.16	0.01	0.11	0.01	-0.03	0.00
Rear attachment width	-0.17	-0.09	-0.18	-0.08	-0.16	-0.01
Median suspensory	-0.08	-0.01	0.03	0.01	0.17	0.02
Udder depth	0.12	0.13	0.14	0.13	0.07	0.02
Udder texture	-0.02	-0.04	-0.05	-0.03	0.00	0.00
Teat length	0.15	0.02	0.18	0.01	0.17	-0.01
Front teat placement	-0.03	0.00	-0.02	-0.01	-0.04	-0.02
Rear teat placement	-0.05	-0.02	0.00	-0.01	0.08	0.00

¹ECMI $_{ij}$ = Maturity rate for ECM between lactation i and j = ECM yield $_j$ - ECM yield $_i$.

²Standard errors of r_g were between 0.09 and 0.15; SE of r_p were all 0.01.

³Standard errors of r_g were between 0.09 and 0.14; SE of r_p were all 0.01.

⁴Standard errors of r_g were between 0.14 and 0.19; SE of r_p were all 0.01.

⁵SCSi = SCS, where i = lactation 1 to 3.

⁶DFS $_i$ = Days to first service, where i = lactation 1 to 3.

†Genetic correlations were significantly different from zero.

of the breeds considered. Fleckvieh and Brown Swiss have a lower genetic potential for milk production and produce, on average, less milk in first lactation; therefore, the effects on udder health are less important.

Fertility traits. The 2 traits used in the fertility analyses (DFS and NRR) were those recommended by Groen et al. (1998b) to describe fertility. Fertility was defined by Darwash et al. (1997) as “the ability of the animal to conceive and maintain pregnancy if served at the appropriate time in relation to ovulation.” The first trait (DFS) is an indicator of observable cyclicity; the second one (NRR) indicates the probability of becoming pregnant at insemination.

Mean DFS was similar to the value reported by Karmideen et al. (2000). Heritability of DFS was in the

same range as Pryce et al. (1998), who also computed a DFS for each of the first 3 lactations. However, it was lower than the heritability of 0.10 found by Schnyder and Stricker (2002) in Swiss Holsteins. Additive genetic correlations between ProdI and DFS in first lactation were negative, except with MilkI12. Correlations estimated with ECM had a larger negative value than those computed with milk. Once again, the importance of the energy needs is seen at the genetic level: cows with genetic potential for low first lactations, when compared with following lactations, start their first ovarian cycle of that lactation sooner than genetically high-producing cows. This result stresses the importance of having good maturity rate values for good fertility. Genetic correlations between ProdI and DFS in second and third lacta-

Table 8. Regression coefficients (b) of daughter production increase records (kg) on their sire EBV for productive life in days (longevity) and presence or absence (1/0) of an insemination during 56 d following insemination (NRR).

Trait	Longevity		NRR	
	b	SE	b	SE
MilkI ¹	0.17	0.02	-175.71	116.60
ECMI ²	0.14	0.02	-228.78	113.57
MilkI12 ³	0.12	0.02	-86.40	123.81
MilkI13	0.20	0.02	-235.25	140.08
MilkI23	0.09	0.02	-148.85	134.00
ECMI12 ⁴	0.10	0.02	-83.88	118.41
ECMI13	0.16	0.02	-325.31	137.36
ECMI23	0.07	0.02	-241.42	129.58

¹MilkI = Production increase for milk = $((2 \times M_2) + (3 \times M_3))/5 - M_1$, where M_x is the milk yield in lactation x , $x = 1, 2$, or 3 .

²ECMI = Production increase for energy-corrected milk (ECM) = $((2 \times ECM_2) + (3 \times ECM_3))/5 - ECM_1$, where ECM_x is the ECM yield in lactation x , $x = 1, 2$, or 3 .

³MilkI_{ij} = Maturity rate for milk between lactation i and j = milk yield _{j} - milk yield _{i} .

⁴ECMI_{ij} = Maturity rate for ECM between lactation i and j = ECM yield _{j} - ECM yield _{i} .

tions were highly variable and had higher standard errors.

Regression of ProdI on NRR was negative. This means that cows that are not re-inseminated in the 56 d following the first insemination have a lower maturity rate than cows that are; in other words, a good ability of becoming pregnant at first insemination is related to a slower maturity rate. This phenomenon may be explained by the positive genetic correlation between NRR and DFS in Swiss Holsteins (Schnyder and Stricker, 2002). This positive correlation means that cows bred soon after calving are more subject to not becoming pregnant at that particular insemination. However, Pryce et al. (1998) and Kadarmideen et al. (2000) found a negative correlation between these traits in UK dairy cows. It must be kept in mind that the NRR correlation in the present study is based on the EBV of the sires, giving high standard errors to the estimates because the EBV are based on binary observations. Moreover, these EBV are computed with insemination records from all lactations and are not values for each of the first 3 lactations. Correlation estimated between ProdI and NRR should be analyzed based on actual cow NRR records of the lactation concerned to get more accurate results. Krogmeier et al. (2003) found no correlation between ProdI and 90-d NRR (0.05 and -0.03 for Fleckvieh and Brown Swiss, respectively) using EBV values for both traits.

Longevity. Regression coefficients of ProdI on sire EBV for longevity were positive and significant. Cows whose sires transmit good longevity had a slightly higher maturity rate than those from sires transmitting

short productive life. Moreover, traits correlated to longevity were also correlated to ProdI. One of these traits is SCS, which was reported to have a correlation of -0.27 to life span (i.e., number of lactations a cow completes) by Pryce and Brotherstone (1999). Another trait positively correlated to both ProdI and longevity is udder depth (Weigel et al., 1997; Pasma and Reinhardt, 1999; Vukasinovic et al., 2002). The structure of the data set reduced the regression of ProdI on longevity because cows culled before the end of the third lactation were not included. Further research should find a way to eliminate the bias in the data set to find a more accurate estimate of the regression or even estimate the correlation between ProdI and longevity.

Conformation traits. Conformation indicates how far a cow "conforms" to the True Type model (Holstein Canada, 2004). This model describes the cow that has the ability to produce large amounts of milk and last in the herd. For this reason, conformation is used as an indicator of longevity. Heritability estimates computed in the present study for conformation traits were in the same range as earlier estimates on Swiss Holsteins (Kadarmideen and Wegmann, 2003) except for stature and heart girth, which were defined differently in the current study (measures in scores instead of centimeters).

Of all conformation traits, chest width has the highest positive correlation to ProdI. This trait is also negatively correlated to milk yield in first lactation (Short and Lawlor, 1992). As first lactation milk yield has a negative weight in the ProdI formula, these cows might often have high ProdI. Moreover, first lactation cows showing width through the front end have a better energy balance throughout lactation and, therefore, less metabolic stress (Veerkamp, 1998). The latter is a hindrance to the increase in production in later lactations.

Of all conformation traits, angularity had the strongest negative correlation to ProdI. Angularity is the trait that often characterizes "milky" animals, as is corroborated by the high correlation between angularity and milk yield in first lactation (0.54; Short and Lawlor, 1992). Conformation of high-producing animals is defined by having more angularity than animals with low production. However, cows showing lots of angularity, because they produce more milk in first lactation, have difficulties in keeping enough energy to grow and, therefore, to be prepared for the production of more milk in the following lactations. Hence, production increases less than for cows showing less angularity.

Selection on ProdI

It would be interesting to know how to include maturity rate in breeding goals. The trait, ProdI, has some

potentially useful correlations for selection. Moreover, there is variance in the PTA of bulls, which enables selection. Correlations to other traits make ProdI a useful functional trait. However, ProdI should not be selected as a single trait. This would lead to cows with low first lactation yield, therefore less profitable cows. Selection on actual production yield should be supplemented by selection on ProdI. The main goal of further research should be the estimation of a precise correlation between ProdI and longevity. This correlation and those already found in this work would enable estimation of the economic value of this trait. Time needed to compute ProdI is also a restriction to the use of that trait. With the current formulas, 2, or eventually 3, lactations have to be finished before a value can be calculated. Selection choices have already been made at that time.

It is important to note that the trait ProdI is defined as the ability of the cow to increase its production gradually from early to later lactations, regardless of actual amount of milk produced within lactations. Persistency, another functional trait, is defined as the ability of cows to sustain a constant level of production at all stages within lactation, whereas ProdI is related to an across-parity gradual increase in yield. Persistency within lactation is a trait that was not considered in the present study. This indication of the "flatness" of the lactation curve is important to select cows with fewer problems at the start of lactation because of a high metabolic stress. Krogmeier et al. (2003) reported a high positive correlation between ProdI and lactation persistency (0.61 for Brown Swiss).

It seems that cows with balanced milk yield throughout lactation show an increase in milk yield over lactations. Flat lactation curves and increases after each lactation should be the ultimate breeding goal from a metabolic stress point of view.

CONCLUSIONS

This study defined a new functional trait related to how cows increase their production potential gradually from early to later lactations, and estimated genetic parameters for it. This included heritabilities and genetic correlations with many important functional traits. Results show that animals can be selected for ProdI, as there is a good genetic variation between bulls and this trait has favorable genetic relationship with economically important functional traits that are currently or soon will be in the dairy cattle breeding goals of many countries (e.g., health, fertility, conformation, longevity). Hence, ProdI, as an indicator of maturity rate, is a potential trait to be included in a breeding goal.

REFERENCES

- Ali, A. K. A., and G. E. Shook. 1980. An optimum transformation for somatic cell concentration in milk. *J. Dairy Sci.* 63:487–490.
- Boettcher, P. J., and B. J. Van Doormaal. 1999. Tools for selection for functional traits in Canada. *Interbull Bull.* 23:29–39.
- Darwash, A. O., G. E. Lamming, and J. A. Woolliams. 1997. Estimation of genetic variation in the interval from calving to postpartum ovulation of dairy cows. *J. Dairy Sci.* 80:1227–1234.
- de Haas, Y., H. W. Barkema, and R. F. Veerkamp. 2002. Genetic parameters of pathogen-specific incidence of clinical mastitis in dairy cows. *Anim. Sci.* 74:233–242.
- Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2001. *ASReml Reference Manual*. Version September 24, 2001. NSW Agriculture, Orange, Australia.
- Groen, A. F., J. Aumann, V. Ducrocq, N. Gengler, J. Soelkner, and E. Strandberg. 1998a. Genetic improvement of functional traits in cattle (GIFT)—An intermediate report. *Proc. Interbull Mtg., Rotorua, New Zealand, Jan. 1998. Interbull Bull.* 17:81–82.
- Groen, A. F., J. Soelkner, J. Aumann, V. Ducrocq, N. Gengler, and E. Strandberg. 1998b. EU Concerted Action "Genetic Improvement of Functional Traits in cattle" (GIFT). *Annu. Rep.* 1997. *Interbull Bull.* 19:9–20.
- Holstein Canada. 2004. History of the true type cow and classification at Holstein Canada. Available: <http://www.holstein.ca/english/Breed/tthistory.asp>. Accessed Jul. 28, 2004.
- Kadarmideen, H. N., R. Thompson, and G. Simm. 2000. Linear and threshold model genetic parameters for disease, fertility and milk production in dairy cattle. *Anim. Sci.* 71:411–419.
- Kadarmideen, H. N., and S. Wegmann. 2003. Genetic parameters for body condition score and its relationship with type and production traits in Swiss Holsteins. *J. Dairy Sci.* 86:3685–3693.
- Kirchgessner, M. 1997. *Tierernährung*. 10. Auflage. Verlags Union Agrar. Germany.
- Krogmeier, D., R. Emmerling, and K. U. Götz. 2003. Leistungssteigerung—ein neues Selektionskriterium in der Rinderzucht? Vortragstagung der DGfZ und der GfT, Göttingen, Germany.
- Lund, T., F. Miglior, J. C. M. Dekkers, and E. B. Burnside. 1994. Genetic relationships between clinical mastitis, somatic cell count, and udder conformation in Danish Holsteins. *Livest. Prod. Sci.* 39:243–251.
- Mrode, R. A., and G. J. T. Swanson. 1996. Genetic and statistical properties of somatic cell count and its suitability as an indirect means of reducing the incidence of mastitis in dairy cattle. *Anim. Breed. Abstr.* 64:847–857.
- Pasman, E., and F. Reinhardt. 1999. Genetic relationships between type composites and length of productive life of black-and-white Holstein cattle in Germany. *Interbull Bull.* 21:117–121.
- Pryce, J. E., and S. Brotherstone. 1999. Estimation of lifespan breeding values in the UK and their relationship with health and fertility traits. *Interbull Bull.* 21:166–169.
- Pryce, J. E., R. J. Esslemont, R. Thompson, R. F. Veerkamp, M. A. Kossabati, and G. Simm. 1998. Estimation of genetic parameters using health, fertility and production data from a management recording system for dairy cattle. *Anim. Sci.* 66:577–584.
- Rupp, R., F. Beaudeau, and D. Boichard. 2000. Relationship between milk somatic cell counts in first lactation and clinical mastitis occurrence in the second lactation of French Holstein cows. *Prev. Vet. Med.* 46:99–111.
- Rupp, R., and D. Boichard. 1999. Genetic parameters for clinical mastitis, somatic cell score, production, udder type traits, and milking ease in first lactation Holsteins. *J. Dairy Sci.* 82:2198–2204.
- Schleppi, Y., and A. Bigler. 2002. Nutzungsdauer und Leistungssteigerung: zwei neue Merkmale für die Stierenselektion. *Schweizer Fleckvieh* 5:37–41.
- Schnyder, U., and C. Stricker. 2002. Genetic evaluation for female fertility in Switzerland. *Interbull Bull.* 29:138–141.

- Short, T. H., and T. J. Lawlor. 1992. Genetic parameters of conformation traits, milk yield, and herd life in Holsteins. *J. Dairy Sci.* 75:1987–1998.
- Uribe, H. A., B. W. Kennedy, S. W. Martin, and D. F. Kelton. 1995. Genetic parameters for common health disorders of Holstein cows. *J. Dairy Sci.* 78:421–430.
- Van der Beek, S. 1999. Breeding for profit in the Netherlands. *Interbull Bull.* 23:75–78.
- VanRaden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. *J. Dairy Sci.* 87:2285–2292.
- Veerkamp, R. F. 1998. Selection for economic efficiency of dairy cattle using information on live weight and feed intake: A review. *J. Dairy Sci.* 81:1109–1119.
- Veerkamp, R. F. 2000. Genetics of energy balance and body condition score. *Metabole stress en de effecten daarvan op voortplanting en gezondheid van landbouwhuisdieren*. NOADD bijeenkomst, Utrecht, The Netherlands.
- Vukasinovic, N., J. Moll, and L. Casanova. 2001. Implementation of a routine genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. *J. Dairy Sci.* 84:2073–2080.
- Vukasinovic, N., Y. Schleppe, and N. Künzi. 2002. Using conformation traits to improve reliability of genetic evaluation for herd life based on survival analysis. *J. Dairy Sci.* 85:1556–1562.
- Weigel, D. J., B. G. Cassell, and R. E. Pearson. 1997. Prediction of transmitting abilities for productive life and lifetime profitability from production, somatic cell count, and type traits in milk markets for fluid milk and cheese. *J. Dairy Sci.* 80:1398–1405.
- Weller, J. I., A. Saran, and Y. Zeliger. 1992. Genetic and environmental relationships among somatic cell count, bacterial infection, and clinical mastitis. *J. Dairy Sci.* 75:2532–2540.