SELECTION FOR BODY WEIGHT IN DAIRY CATTLE

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SELECTION FOR BODY WEIGHT IN DAIRY CATTLE

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Abstract

This thesis is on the possibilities and relevance of selection strategies for dairy cattle that include information on body weight. Genetic parameters are estimated for body weight, dry-matter intake capacity and body condition score. Analyses of experimental and field data show that genetic levels for body weight can efficiently be changed by selection using conformation data. Dry-matter intake capacity and body condition score have a moderate heritability. For Dutch production circumstances, the economic value is negative for body weight but positive for dry-matter intake capacity. The relevance of body weight for selection strategies with milk production and dry-matter intake capacity highly depends largely on the economic value of dry-matter intake capacity and reliability of breeding values for dry-matter intake capacity. Although the weighting in the breeding goal for body weight is negative, a negative weighting of breeding values for body weight cannot be recommended for present Dutch production circumstances.

Stellingen

1. De grote genetische variatie voor lichaamsgewicht en de beschikbaarheid van standaard vastgelegde exterieurgegevens maken een effectieve en efficiënte selectie op lichaamsgewicht mogelijk.
   (Dit proefschrift).

2. Ondanks de negatieve economische waarde voor lichaamsgewicht in het fokdoel is een negatieve weging van fokwaarden voor lichaamsgewicht zonder rekening te houden met voeropname-capaciteit niet aan te bevelen.
   (Dit proefschrift).

3. Intensieve selectie op fokwaarden van de ouders voorafgaand aan de centrale hengstenkeuring kan de huidige genetische vooruitgang in sportkenmerken voor KWPN rijpaarden aanzienlijk verhogen.

4. Toenemende concurrentie tussen onderzoeksgroepen bedreigt de geschiktheid van het 'Peer Review'-systeem voor de beoordeling van wetenschappelijke artikelen.

5. De Wet Modernisering Universitaire Bestuursorganisatie (*Stb.* 1997, 117) plaatst ten onrechte de democratische rechten van studenten en personeel terug in de tijd.

6. De mobiliteit van universiteitsmedewerkers moet verder gaan dan het jaarlijks veranderen van werkkamer.

7. De aftrekbaarheid van hypotheekrente volgens progressieve belastingtarieven is, anders dan de toekenning van aandelenopties, een vorm van exorbitante zelfverrijking.

Stellingen bij het proefschrift van E.P.C. Koenen
'Selection for body weight in dairy cattle'
Wageningen, 2 maart 2001.

CONTENTS

CHAPTER 1

General introduction

The general aim of a livestock breeding strategy is to produce a new generation of animals that better fits the breeding goal than the present generation. In dairy cattle, emphasis is gradually shifting from increasing output per cow to reducing costs and improving efficiency of production.
Until now, selection for gross feed efficiency is generally ignored when making selection decisions as the correlated response to selection for increased milk yield results in 70-95% of the potential improvement that could be achieved through direct selection for gross feed efficiency (Kennedy, 1984). Nevertheless, biological and economic efficiency of dairy production might be improved further when genetic variation in feed costs is considered, as feed costs constitute a large proportion of the total costs. Feed intake is mainly used to meet energy and protein requirements for growth, maintenance, pregnancy and milk production. The proportion of energy requirements for maintenance is substantial: e.g. a cow with a mature milk production of 6700 kg/year and a mature body weight (BW) of 600 kg allocates 43% of the total energy input to maintenance during her entire life (Korver, 1988). As maintenance requirements directly depend on BW (Agricultural Research Council, 1980), information on BW provides information on the biological and economic efficiency of dairy production. The inclusion of genetic information on BW in selection decisions might be a tool to improve the economic response of selection (McDaniel and Legates, 1965; Yerex *et al.*, 1988). Studies in New Zealand (Dempfle, 1989; Spelman and Garrick, 1997) evaluated the effect of including information on BW in the breeding scheme and found that the economic response by selection could increase up to 4%. For Dutch production circumstances, Steverink *et al.* (1993) found that the economic response could increase up to 2% when information on BW is used in selection. Although information on BW is a potential additional tool to increase economic response by selection, it is not yet routinely considered in most breeding programs (INTERBULL, 1996). The successful implementation of a selection strategy that optimally includes information on BW is hindered by limited knowledge on procedures for data recording, genetic evaluation and combined selection decisions.

SELECTION FOR BODY WEIGHT

Data recording and genetic evaluation

The availability of reliable estimated breeding values (EBVs) for potential breeding animals is one of the prerequisites for an efficient selection for BW. It is therefore important to optimise procedures for data recording and genetic evaluation of BW. As the main interest in BW originates from the direct relation to maintenance requirements, observations on BW should provide a good measurement of mean BW during lifetime. The number of observations that is needed per animal to obtain a good estimate for mean BW depends on the repeatability. The repeatability of an observation indicates the relevance of multiple observations: a high repeatability implies that extra observations contribute only a limited amount of additional information.

A genetic evaluation of BW observations requires knowledge on adjustment factors and accurate estimates for the genetic parameters. Heritability estimates for BW are numerous and are mostly in the range 0.4 to 0.5 (Veerkamp, 1998). However, these estimates often originate from small-scale experiments and are therefore less suitable for the evaluation of BW observations from a routine large-scale recording system. Heritability estimates for BW observations from large-scale recording system are scarce. When genetic variation in BW is large enough to introduce a large-scale recording system for BW, indirect information from related traits such as body measurements and conformation traits might for practical reasons be more attractive than direct information from weighing cows. Several studies (e.g. Vos and Vos, 1967; Heinrichs *et al.*, 1992) reported high phenotypic correlations between body measurements and BW. However, estimates for the genetic correlations are scarce.

Most studies on the heritability for BW assumed that the genetic background for BW is constant across all life-stages, i.e. the genetic variance for BW is constant in time and genetic correlations between BW observations at different ages equal unity. However, the genetic background of BW might vary with age or lactation stage as changes in BW are related to various biological processes such as growth, lactation and body tissue (de)mobilisation. This means that the dynamic aspects of the genetic background of BW have to be studied, especially when observations of growing and lactating animals are included.

Combined selection

Maximum genetic improvement of dairy cattle is only obtained when the selection strategy optimally combines EBVs on all relevant traits. To facilitate efficient selection of breeding animals, breeding organisations already estimate and publish breeding values for various traits. These EBVs are presented per trait or are combined in part or overall in a summarising economic index (Hazel, 1943). The optimal relative weighting of EBVs within a combined selection strategy also depends on the effect of genetic improvement on economic efficiency. The economic value (EV) of a trait expresses the extent that economic efficiency of production is improved by an increase of that trait at the moment of expression.

The EV for BW is generally reported to be negative (e.g. Dempfle, 1989; Groen, 1989). On the one hand, a lower BW is preferred to reduce feed input for maintenance requirements; on the other hand, a higher BW results on average in higher revenues from beef production. The EV of BW varies with variation in feed costs, beef prices and other production circumstances (Groen, 1989; Visscher *et al.*, 1994). As future production circumstances are uncertain, estimates for the EVs under alternative production circumstances have to be considered when deciding on a selection strategy.

Combined selection on milk and BW with a negative weighting on BW results in lower responses in milk production, dry-matter intake capacity (DMIC) and body condition score (BCS) (Groen and Korver, 1990; Veerkamp, 1998). More knowledge on the consequences of this correlated change in DMIC is desired. First, earlier studies showed that a large DMIC is favoured as it facilitates the increase of the proportion of roughage in the diet (Groen and Korver, 1989). Secondly, DMIC is one of the components that relate to the energy balance (EB), which represents net energy intake minus net energy requirements. A possible increase of the negative EB in early lactation is undesired as a more negative EB generally relates to health and fertility problems (e.g. Bulter and Smith, 1989). As direct observations on EB are not available, observations on BCS might be an indirect measurement of the EB and might therefore provide helpful information when defining a combined selection strategy. Consequently, a study on selection for BW should consider genetic parameters of DMIC and BCS as well.

Finally, when estimates for the genetic and phenotypic parameters of the breeding goal traits and their corresponding EVs are available, the optimal combined selection strategy can be derived.

AIMS AND OUTLINE OF THIS THESIS

The first aim of this thesis is to study the possibilities for a large-scale genetic evaluation for BW. The second aim is to evaluate selection strategies that optimally combine EBVs for milk production and BW.

First, adjustment factors for environmental effects and repeatabilities of BW observations of growing and lactating heifers are estimated. Chapter 2 focuses on the effect of age on BW of growing heifers until first calving. Chapter 3 studies several non-genetic adjustment factors and estimates repeatabilities for BW during the first three parities. Estimates for the non-genetic effects from Chapter 2 and 3 indicate what effects need to be considered in a genetic evaluation for BW. Furthermore, repeatability estimates for BW provide information on the optimal moment and frequency of data collection.

Secondly, genetic parameters for BW, BCS and DMIC are estimated. Chapter 4 evaluates observations on BW and conformation traits on lactating heifers from field data. This analysis provides information on the suitability to base a routine genetic evaluation for BW on conformation traits. In Chapter 5, the dynamics of the genetic background of BW, BCS and DMIC of lactating heifers are estimated from repeated observations using covariance function methodology. In Chapter 6, genetic correlations between size and milk production during the first lactation are estimated from field data. Genetic parameters for routinely collected observations on BCS are estimated in Chapter 7.

Thirdly, EVs for BW and DMIC under current and alternative production circumstances are estimated in Chapter 8. This Chapter includes three scenarios to model future production circumstances. For these alternative production circumstances, EVs for BW and DMIC are derived at farm level.

Finally, possibilities and relevance of including BW information in a breeding program are discussed for the Dutch breeding program in Chapter 9. In this Chapter, selection responses and economic efficiency of alternative selection strategies are compared.

REFERENCES

Agricultural Research Council, 1980. *The nutrient requirements of ruminant livestock.* Commonwealth Agricultural Bureaux. Slough, England. 351 pp.

Butler, W.R. and R.D. Smith, 1989. Interrelationships between energy balance and postpartum reproductive function in dairy cattle. *J. Dairy Sci.* 72: 767-783.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Groen, A.F., 1989. Economic values in cattle breeding. I. Influences of production circumstances in situations without output limitations. *Livest. Prod. Sci.* 22: 1-16.

Groen, A.F. and S. Korver, 1989. The economic value of feed intake capacity of dairy cows. *Livest. Prod. Sci.* 22: 269-281.

Groen, A.F. and S. Korver, 1990. Feed intake capacity of lactating cows in dairy and dual purpose cattle selection. *J. Anim. Breed. Genet.* 107: 389-396.

Hazel, L.N., 1943. The genetic basis for constructing selection indexes. *Genetics* 28: 476-490.

Heinrichs, A.J., Rogers G.W. and J.B. Cooper, 1992. Predicting body weight and wither height in Holstein heifers using body measurements. *J. Dairy Sci.* 75: 3576-3581.

INTERBULL, 1996. *Sire evaluation procedures for non-dairy-production and growth & beef traits practised in various countries.* INTERBULL bulletin no. 13. Intern. Bull Evaluations Service. Uppsala, Sweden. 201 pp.

Kennedy, B.W., 1984. Breeding for efficiency: swine and dairy cattle. *Can. J. Anim. Sci.* 64: 505-512.

Korver, S., 1988. Genetic aspects of feed intake and feed efficiency in dairy cattle:

a review. *Livest. Prod. Sci.* 20: 1-13.

McDaniel, B.T. and J.E. Legates, 1965. Associations between body weight predicted from heart girth and production. *J. Dairy Sci.* 48: 947-956.

Spelman, R.J. and D.J. Garrick, 1997. Effect of live weight and differing economic values on responses to selection for milk fat, protein, volume and live weight. *J. Dairy Sci.* 80: 2557-2562.

Steverink, M.H.A., Van Arendonk, J.A.M., Berentsen, P.B.M. and A.F. Groen, 1993. *Gecombineerde selectie op melkproduktiekenmerken en lichaamsgewicht.* Report Department of Animal Breeding, Wageningen Agricultural University. Wageningen, The Netherlands. 32 pp.

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.

Visscher, P.M., Bowman, P.J. and M.E Goddard, 1994. Breeding objectives for pasture based dairy production systems. *Livest. Prod. Sci.* 40: 123-137.

Vos, M.P.M. and H. Vos, 1967. Schatting van het levend gewicht van runderen met behulp van lichaamsmaten. *Tijdschr. Diergeneesk.* 92: 1073-1081.

Yerex, R.P., Young, C.W., Donker, J.D. and G.D. Marx, 1988. Effects of selection for body size on feed efficiency and size of Holsteins. *J. Dairy Sci.* 71: 1355-1360.

CHAPTER 2

Genetic analysis of growth patterns of Black-and-White dairy heifers

E.P.C. Koenen and A.F. Groen

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ABSTRACT

Monthly body weight (BW) to the age of 600 days along with BW at first calving of 743 heifers were analysed to estimate the genetic relationship between BW at first calving and other growth variables. The Von Bertalanffy function and a two-phase logistic function were used to fit growth patterns of individual heifers. The two-phase logistic function fitted the data more adequately than did the Von Bertalanffy function. Calves from first parity dams were born at a lower degree of maturity than calves from third parity dams. Calves with a high proportion of Holstein-Friesian genes had a higher BW both at first calving and at maturity. Heritabilities of the variables of the Von Bertalanffy and the two-phase logistic function ranged from 0.02 to 0.31 and 0.15 to 0.26, respectively. Estimated mature BW showed a highly negative correlation with rate of maturation (–0.56 to –0.82). The BW at first calving showed a very high genetic correlation (0.74 to 0.90) with estimated mature BW and a negative correlation with maturation rate (–0.18 to –0.40). Results of this study indicated that BW at first calving can be used as an indirect trait when mature BW is included in the breeding goal.

INTRODUCTION

The body weight (BW) of dairy cattle has a negative economic value; marginal costs associated with increased energy requirements for raising female stock and increased maintenance requirements for lactating cows exceed marginal revenues from increased BW of disposed young female stock and lactating cows (VanRaden, 1988; Dempfle, 1989; Groen, 1989; Steverink *et al.*, 1993; Visscher *et al.*, 1994). Economic value of BW might become even more negative if more stringent environmental restrictions are imposed (Steverink *et al.*, 1994). Reports from New Zealand (Dempfle, 1989) and The Netherlands (Steverink *et al.*, 1993) evaluated the economic impact of inclusion of BW in the breeding goal with production traits. Expected increase in profitability was 2 to 4% when BW was included in the breeding goal and in the selection index. In those reports, the breeding goal included mature BW, which cannot be recorded before about 4 to 5 years of age (Hietanen and Ojala, 1995).

For practical reasons, early information about mature BW is desirable. The BW at first calving might be used as an indirect trait to select for mature BW. Inclusion of BW at first calving is useful in a selection index when genetic correlation is high between BW at first calving and mature BW. Mathematical functions can be used to derive parameters for growth and to study the genetic relationships of these parameters. Studies of beef cattle (Brown *et al.*, 1972; Fitzhugh, 1976; DeNise and Brinks, 1985) demonstrated that selection for BW at immature stages affects mature BW and has an impact on other growth variables, such as the maturation rate and BW at birth. The impact of selection on BW at an immature stage on mature BW and other growth characteristics of dairy cattle is not known. This study evaluated the genetic correlation of BW at first calving with estimated mature BW and estimated genetic parameters for relationships among growth curve variables.

MATERIALS AND METHODS

Data

Data on 969 heifers from the experimental farm of Wageningen Agricultural University were collected from November 1982 through February 1995. Breeds of the animals were Dutch Black-and-White (DBW), Holstein-Friesian (H) and crossbreds of DBW and H. Newborn heifers were fed colostrum for *ad libitum* intake for 3 days. During next 7 weeks, heifers were fed 4 litres of milk daily with hay for *ad libitum* intake. From 8 to 26 weeks, heifers received 1 kg of concentrate (6.6 MJ of NE_L/kg of DM) and hay for *ad libitum* intake. During summer, heifers were kept on pasture; during winter, heifers were fed hay and grass silage for *ad libitum* intake. Heifers were bred when they were 14.5 months without restrictions on BW. Yearly calving season was from November through May. All newborn calves and their dams were weighed once a week; all other animals were weighed monthly. Repeated measurements of the same animal within 25 days after birth were deleted because the error components of repeated observations within a very short period are expected to have a large autocorrelation. To reduce bias from effects of gestation, data were limited to BW up to 600 days of age. Effect of pregnancy on BW at this age was expected to be minimal (Bereskin and Touchberry, 1967; Silvey and Haydock, 1978). Heifers with less than 18 observations were deleted. Additionally, BW at first calving was included. Average age at first calving was 737 days (s.d. 23). After editing, 767 heifers remained, for a total of 15,132 observations.

Growth curves

In a preliminary study, Gompertz, Von Bertalanffy, Michaelis-Menten, logistic and Richards functions were compared. Properties of these functions were discussed by Brown *et al.* (1972), Fitzhugh (1976), Koops (1986) and Perotto *et al.* (1992). To compare the goodness of fit of these functions, residual sums of squares and estimates of the fitted variables were considered. The Von Bertalanffy function fitted the data best and was used for further analyses.

The Von Bertalanffy function was represented by:

$$y_t \quad = \quad A\,(1 - B\,e^{-kb\,t})^3$$

where

y_t = BW (kg) at age t (days),

A = asymptotic mature BW (kg),

B = constant of integration, and

kb = maturation rate.

The B parameter is correlated with stage of maturity at birth. When stage of maturity is defined as the proportion of actual BW to mature BW, stage of maturity at birth equals $(1 - B)^3$, that is, a small B-value represents a higher stage of maturity at birth.

The kb parameter is related to the increase in stage of maturity and can be interpreted biologically as a maturing index (Perotto *et al.*, 1992). At the Von Bertalanffy function, kb = 27/12 times the maximum increase in stage of maturity. When two animals are growing to a similar mature BW, differences in maturation rate equal differences in absolute growth. The Von Bertalanffy function has a fixed inflection at which maximum growth occurs. Maximum growth rate is fixed by the fitted A, B and kb values and occurs when 8/27 of mature BW is reached. All previously mentioned functions are characterised by having one inflection point. Brody and Ragsdale (1921) showed the presence of two stages of maximum growth in the growth curve of dairy cattle. Koops (1989) applied logistic functions to describe multiphasic growth patterns. In this study, the following two-phase growth function (Koops, 1986) was used:

$$y_t = \frac{a_1}{1+e^{-km(t-b_1)}} + \frac{a_2}{1+e^{-km(t-b_2)}}$$

where

y_t = BW (kg) at age t (days),

a_1 = asymptotic BW during the first phase (kg),

b_1 = age at the first inflection point (days),

km = maturation rate,

a_2 = asymptotic BW during the second phase (kg), and

b_2 = age at the second inflection point (days).

This growth function is based on the summation of two sigmoidal curves that partly overlap. Asymptotic mature BW is estimated by $(a_1 + a_2)$. The km parameter of the two-phase logistic function equals four times the maximum increase in maturity. Maturation rate was equal for both phases. When different maturation rates were fitted for both phases separately, data of many animals did not converge. The estimated rate of maturation during the first phase did not differ significantly from the estimated rate of maturing during the second phase. In agreement with findings of Koops (1989), paired dependencies between parameter estimates decreased when equal rates of maturing were used for both phases.

Statistical analysis

The NLIN procedure of SAS® (1990) with the DUD option was used to estimate the parameters of both curves for each heifer (n = 767). To compare the goodness of fit, the average residual sum of squares were considered. Animals with an estimated mature BW greater than 1000 kg were deleted. After exclusion of these animals, 743 remained. The Durbin-Watson statistic (Durbin and Watson, 1951) was used to test for autocorrelation among residuals.

Two additional variables per heifer were calculated, estimated BW at first calving based on the Von Bertalanffy function and estimated BW at first calving based on the two-phase logistic function. Variables were based on individual estimated parameters and on actual age at first calving of the heifer.

Estimated variables of the Von Bertalanffy (A, B and kb), the two-phase logistic (a_1, b_1, km, a_2, b_2 and $a_1 + a_2$), recorded BW at first calving and estimated BW at first calving were considered as new traits. Least-squares analysis was used on these 12 traits to test for significance of fixed effects season by year of birth, proportion of H genes and parity of dam using the MIXED procedure (SAS®, 1990) with sire as a random effect. Three parities of dam groups were defined, first (n = 280 heifers), second (n = 204) and third or greater parity (n = 259) and five groups of month of birth were used, November through December (n = 145 heifers), January (n = 162), February (n = 165), March (n = 180) and April through May (n = 91). Five genetic groups of heifers were defined: 0% H (n = 35 heifers), 1 to 25% H (n = 19), 26 to 50% H (n = 156), 51 to 75% H (n = 205) and >75% H (n = 328). Groups not only accounted for additive effects but might also have corrected for some heterosis effects and recombination losses.

To estimate genetic parameters of all 12 traits, the following model was used:

$$y_{ijkl} = \mu + ys_i + hf_j + par_k + ani_l + e_{ijkl}$$

where

y_{ijkl} = observation on the trait,
μ = overall mean,
ys_i = fixed effect of the year-season (52 levels),
hf_j = fixed effect of the HF group (5 levels),
par_k = fixed effect of the parity of dam (3 levels),
ani_l = random effect of the animal (743 levels) and
e_{ijkl} = random residual term.

An additive genetic relationship matrix with pedigrees up to six generations was included in the analyses. Estimates of variance components were obtained by a REML method using a derivative-free algorithm (Graser *et al.*, 1987). Using the DFREML software package (Meyer, 1991), the simplex procedure was employed to locate the maximum of the log likelihood. Convergence was considered to have been reached when the variance of $-2\times\log(\text{likelihood})$ for the simplex points was $<10^{-8}$. Genetic and phenotypic correlations among traits were estimated from bivariate analyses using starting values from univariate analyses. Because the same model was applied to all traits and observations on all traits were available, a canonical transformation (Meyer, 1985) was used to reduce computational effort. Standard errors of genetic correlations were approximated according to methods of Falconer (1989).

RESULTS

Curve fitting

In total, 743 of 767 animals had valid estimates for both functions. Mean sums of squares of the residuals were 2728 and 1384 for the Von Bertalanffy and the two-phase logistic functions, respectively. The Durban-Watson statistic had positive autocorrelation ($P < 0.05$) for 715 animals fitted by the Von Bertalanffy function. However, when the two-phase logistic function was fitted, only one animal had a significant autocorrelation.

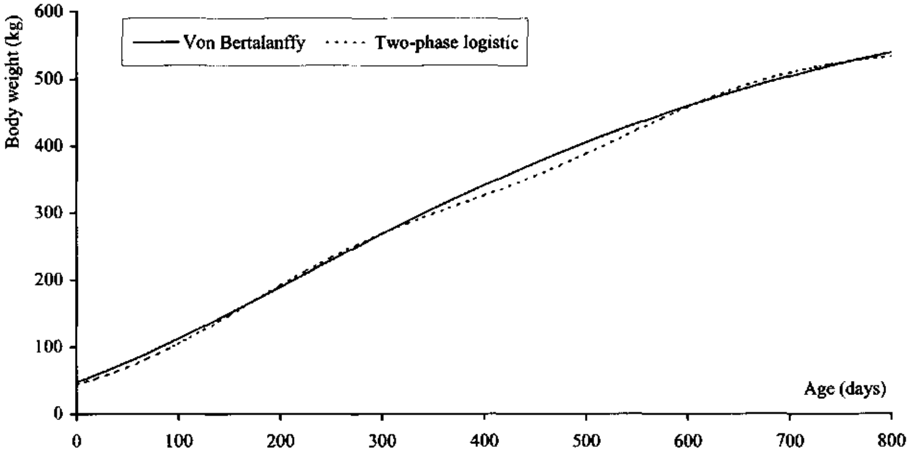

Figure 1. Mean BW of heifers fitted by the Von Bertalanffy function and the two-phase logistic function based on unadjusted means.

Table 1. Unadjusted means, phenotypic standard deviations (σ_p), ranges and estimated contrasts for parity of the dam and genetic groups of variables of the Von Bertalanffy function, the two-phase logistic function, calving weight (CW), CW estimated by the Von Bertalanffy function (CWB) and CW estimated by the two-phase logistic function (CWT) (n = 743).

				Contrast	
				Parity	Holstein proportion
Variable[1]	Mean	σ_p	Range	≥3 *vs.* 1	>75% *vs.* 0%
Von Bertalanffy					
A	667	96.6	437 – 987	6.73	17.6
B	0.586	0.0235	0.517 – 0.678	–0.0151***	–0.00575
kb	0.00269	0.0005	0.0014 – 0.0049	–0.000047	–0.0000175
Two phase logistic					
a_1	309	41.9	166 – 480	4.32	13.10
b_1	161	29.5	65 – 404	–8.20	–4.03
km	0.01128	0.00157	0.00572 – 0.0155	–0.000141	0.000108
a_2	237	48.2	32.0 – 583	3.87	13.226
b_2	550	81.1	130 – 1075	–3.20	–1.66
$a_1 + a_2$	546	65.5	388 – 941	8.09	25.3
CW	508.0	38.3	390 – 631	7.47	19.9
CWB	501.9	38.3	393 – 630	7.45	19.8
CWT	507.9	39.1	386 – 628	7.22	20.3

[1] A = asymptotic mature BW, B = constant of integration, kb = maturation rate, a_1 = asymptotic BW during the first phase, b_1 = age at the first inflection point, km = maturation rate, a_2 = asymptotic BW during the second phase, b_2 = age at the second inflection point and $a_1 + a_2$ = asymptotic mature BW.

The Von Bertalanffy and the two-phase logistic function are in Figure 1 using unadjusted means of the variables. Unadjusted means, phenotypic standard deviations, ranges and estimated contrasts for the parity of the dam and genetic groups of the parameters of both are in Table 1.

Estimated mature BW (A) of 667 kg and estimated constant of integration (B) of 0.586 of the Von Bertalanffy function implied a mean BW at birth of 47 kg (= 667 × $(1 - 0.586)^3$). Maximum growth rate in the Von Bertalanffy curve (Figure 1) equals 800 g/day and was reached at 212 days of age. The two-phase logistic function had inflection points at 161 and 550 days during the first and second phases, respectively. Asymptotic BW of first and second phases were 308 and 238 kg, respectively, resulting in an asymptotic BW of 546 kg. Maximum daily growth during the first and second phases was estimated at 871 and 666 g/day, respectively. When both phases were combined, daily growth was maximal at 169 days of age (897 g/day of growth) and 537 days (713 g/day). Within both maxima, minimum growth occurred at 375 days of age (552 g/day). Mean BW at first calving was 508 kg and estimated BW at calving were 502 and 508 kg for the Von Bertalanffy and the two-phase logistic functions, respectively.

Fixed effects

To illustrate the effects of parity of the dam and genetic group, extreme contrasts are presented in Table 1. Estimated mature BW was 7 to 8 kg higher at third parity than at first parity for both functions. Increased parity decreased ($P < 0.001$) the integration constant of the Von Bertalanffy function. Increased parity of the dam was correlated with a lower maturation rate for both the Von Bertalanffy function and the two-phase logistic function. The two-phase logistic function illustrated that maximum absolute growth of the first phase was reached earlier ($P < 0.001$) for calves from third parity dams than for calves from first parity dams.

A high proportion of H genes was correlated with an increased BW at calving and at maturity. The effects of a high proportion of H genes on stage of maturity at birth and on maturation rate were not significant ($P > 0.10$).

Genetic parameters

Genetic parameters of the variables of the Von Bertalanffy function are in Table 2. Heritabilities were moderate (0.21 to 0.31) for mature BW and constant of integration but very low (0.02) for maturation rate. A high negative genetic correlation (−0.82) was found between mature BW and maturation rate, implying that heavier heifers mature slower. The genetic correlation was moderate (0.19)

Table 2. Estimated heritabilities (diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) of the variables of the Von Bertalanffy function and corresponding standard errors.

	A	B	kb
A[1]	0.21 ± 0.07	0.27	–0.59
B	0.19 ± 0.20	0.31 ± 0.08	0.05
kb	–0.82 ± 0.21	–0.01 ± 0.57	0.02 ± 0.05

[1] A = asymptotic mature BW, B = constant of integration and kb = maturation rate.

between mature BW and constant of integration, indicating that heifers with a large mature BW had, on average, less maturity at birth than heifers with a lower mature BW. Constant of integration and maturation rate were not genetically correlated (–0.01).

Genetic parameters of the variables of the two-phase logistic function are in Table 3. Heritabilities ranged from 0.15 to 0.26. Maturation rate was highly correlated (–0.83 to –0.91) with age at first and second inflection points. Rate of maturing was highly correlated (–0.75) with asymptotic BW of the first phase, but nearly uncorrelated (–0.14) with asymptotic BW during second phase. Genetic correlation of maturation rate and estimated mature BW is –0.56. Age at maximum growth in both phases is positively correlated (0.45 to 0.47) with mature BW. Because of autocorrelation, phenotypic and genetic correlations were very high between asymptotic BW in separate phases and asymptotic mature BW.

Estimated heritability of weight at calving was 0.48. Heritabilities of estimated BW at calving were 0.60 and 0.51 for the Von Bertalanffy function and the two-phase function, respectively. Phenotypic and genetic correlations of the parameters of the Von Bertalanffy function with BW at first calving and with estimated mature BW are in Table 4. High genetic correlations (0.90 to 0.97) between calving BW, estimated calving BW, and mature BW were estimated. The constant of integration had a low to moderate correlation with calving BW (–0.34 to 0.17). Genetic correlation between rate of maturing and calving BW was highly negative (–0.54 to –0.66).

Recorded BW at first calving had a high genetic correlation with maximum BW during the two phases (0.48 to 0.74) and with mature BW (0.74) estimated by the two-phase logistic function (Table 5). Genetic correlation between estimated BW at calving and estimated mature BW was very high (0.93), possibly because of autocorrelation. Negative correlations between BW at calving and ages at inflection points were low (–0.16 to 0.03). Calving BW had only a small negative correlation (–0.05 to –0.07) with maturation rate.

Table 3. Estimated heritabilities (diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) of the variables of the two-phase logistic function.

	a_1	b_1	km	a_2	b_2	$a_1 + a_2$
a_1[1]	0.26 ± 0.08	0.75	–0.60	0.04	0.66	0.65
b_1	0.56 ± 0.21	0.22 ± 0.07	–0.73	–0.03	0.56	0.60
km	–0.75 ± 0.09	–0.83 ± 0.06	0.26 ± 0.07	–0.06	–0.54	–0.42
a_2	0.39 ± 0.21	0.39 ± 0.21	–0.14 ± 0.16	0.15 ± 0.06	0.38	0.78
b_2	0.56 ± 0.15	0.87 ± 0.05	–0.91 ± 0.03	0.31 ± 0.22	0.24 ± 0.07	0.70
$a_1 + a_2$	0.83 ± 0.07	0.45 ± 0.18	–0.56 ± 0.14	0.82 ± 0.08	0.47 ± 0.17	0.26 ± 0.08

[1] a_1 = asymptotic BW during the first phase, b_1 = age at the first inflection point, km = maturation rate, a_2 = asymptotic BW during the second phase, b_2 = age at the second inflection point and $a_1 + a_2$ = asymptotic mature BW.

Table 4. Phenotypic (r_p) and genetic (r_g) correlations of the variables of the Von Bertalanffy function with weight at first calving (CW) and with estimated weight at first calving (CWB).

	CW		CWB	
	r_p	r_g	r_p	r_g
A	0.72	0.90 ± 0.03	0.73	0.97 ± 0.01
B	0.01	–0.34 ± 0.13	0.15	0.17 ± 0.13
kb	–0.40	–0.54 ± 0.32	–0.36	–0.66 ± 0.23

[1] A = asymptotic mature BW, B = constant of integration and kb = maturation rate.

Table 5. Phenotypic (r_p) and genetic (r_g) correlations of the variables of the two-phase logistic function with weight at first calving (CW) and with estimated weight at first calving (CWT).

	CW		CWT	
	r_p	r_g	r_p	r_g
a_1[1]	0.53	0.74 ± 0.07	0.52	0.72 ± 0.07
b_1	0.10	–0.16 ± 0.16	0.13	0.03 ± 0.16
km	–0.18	–0.07 ± 0.15	–0.14	–0.05 ± 0.14
a_2	0.52	0.48 ± 0.14	0.57	0.55 ± 0.12
b_2	0.26	–0.09 ± 0.15	0.22	–0.13 ± 0.15
$a_1 + a_2$	0.72	0.74 ± 0.07	0.72	0.93 ± 0.02

[1] a_1 = asymptotic BW during the first phase, b_1 = age at the first inflection point, km = maturation rate, a_2 = asymptotic BW during the second phase, b_2 = age at the second inflection point and $a_1 + a_2$ = asymptotic mature BW.

DISCUSSION

Fitting of curves

This study estimated the relationships of BW at first calving with mature BW and other growth variables of dairy cattle. Because mature BW is hard to record directly, mature BW of an individual was estimated by extrapolating longitudinal data. The relationship between BW at first calving and other variables of the growth function could only be estimated accurately when the applied growth function fitted the data adequately. When the Von Bertalanffy function was fitted, many heifers showed positive autocorrelation, indicating systematic underestimation or overestimation of BW. Graphic representation of the residuals showed that the Von Bertalanffy function overestimated BW systematically until the age of about 200 days. In this study, the estimated birth BW of 47 kg was higher than the mean recorded birth BW of 40 kg reported by Groen and Vos (1995) using some of the same data. Overestimation of birth BW by the Von

Bertalanffy function was in agreement with results of Goonewardene *et al.* (1981) and Brown *et al.* (1976). One explanation for systematic overestimation of BW early in life might be the estimation procedure. In this study, a least squares method was used, assuming equal error variances during the growth period. However, error variances (e.g. gut fill) might increase during growth.

Maximum absolute growth for the two-phase logistic function was found for 6 and 18 months of age, which was comparable with reported maximum growth in the growth curve of dairy cattle at about 5 months and at about 20 months (Brody and Ragsdale, 1921). In this study, only two phases were fitted, based on monthly weighings up to 600 days of age and based on BW at first calving. In a study by Koops (1989), three growth phases were fitted when BW at second calving was also included. To detect individual growth phases, frequently measured BW at different ages in a wide range are needed. When a three-phase function was fitted to the data of this study, parameters did not reach convergence for most animals. Because the third growth phase was outside the range of observations, estimated mature BW might have been underestimated.

Meijering and Postma (1985) and Groen and Vos (1995) found a higher birth BW as parity of dam increased and as proportion of H genes increased. Differences in birth BW can be explained by differences in mature BW and by differences in degree of maturity at birth. The constant of integration of each individual heifer was used to calculate the degree of maturity at birth. Average degree of maturity was 0.072 (s.d. 0.012). The effect of parity on degree of maturity at birth was significant ($P < 0.001$), but the effect of H group was not ($P > 0.05$). This difference in results suggested that differences in birth BW of calves from third parity heifers were due to differences in stage of maturity and a slightly higher mature BW, but differences in birth BW of H calves were mainly due to higher mature BW. At the start of the experiment, BW at second calving was also recorded for 37 animals. Mean BW at second calving was 529 (s.d. 48) kg, at an average age of 1096 (s.d. 35) days. Age at second calving was used to estimate BW at second calving using the Von Bertalanffy function and the two-phase logistic function: 607 and 545 kg, respectively, suggesting a better fit for the two-phase logistic function outside the range of observations.

Genetic parameters

Estimated heritabilities of BW at first calving of H heifers reported by Lin *et al.* (1985) and Lee *et al.* (1992) ranged from 0.28 to 0.37. In both studies, data were recorded in multiple herds. In our study, data were limited to only one herd, and reduced environmental variance might explain the higher estimated heritability of 0.48. Groen and Vos (1995) reported a heritability of 0.61. The BW at first calving estimated by growth functions showed higher heritabilities than BW at calving, which might be explained by differences in the amount of data used. The BW at calving consists of one observation, but estimated BW at calving is based on more.

Estimated heritabilities of BW at fixed immature ages (Groen and Vos, 1995) were higher than the heritability of estimated asymptotic BW. With immature heifers, differences in BW at a fixed age were caused not only by differences in mature BW but also by differences in degrees of maturity. Heritabilities for degree of maturity were moderate to high. Even among animals of similar mature BW, considerable genetic variation in degree of maturity at fixed ages exists (Fitzhugh and Taylor, 1971). Our results confirmed findings of studies of beef cattle (Brown *et al.*, 1972; DeNise and Brinks, 1985) that reported a negative correlation of maturation rate with mature BW. Genetic correlations of BW at calving with mature BW were high, indicating that BW at first calving could be used as an index trait for selection on mature BW.

At present, BW at first calving is not included in field recording for most breeding schemes. When recording of BW is intended to be combined with the regular field recording system of production traits of heifers, some issues must be considered. Effects of gestation and lactation can largely influence the BW (Hietanen and Ojala, 1995). When heifer data are used, adequate corrections for these effects have to be made. Moreover, the repeatability of measurement needs to be evaluated. The repeatability of BW for different periods might indicate the optimal frequency and the optimal period for measuring BW. Field recording might be facilitated by using indirect measurements of BW (e.g. body measurements such as heart girth and wither height) (Gravir, 1967; Heinrichs *et al.*, 1992).

Body weight at first calving has a high positive correlation with mature BW, indicating that BW at first calving can be used in a selection index to select successfully for mature BW. Further studies are needed for implementation of BW with field recording systems.

REFERENCES

Bereskin, B. and R.W. Touchberry, 1967. Some effects of pregnancy on body weight and paunch girth. *J. Dairy Sci.* 50: 220-224.

Brody, S. and C. Ragsdale, 1921. The rate of growth of the dairy cow - extrauterine growth in weight. *J. Gen. Physiol.* 3: 623-633.

Brown, J.E., Brown, C.J. and W.T. Butts, 1972. A discussion of the genetic aspects of weight, mature weight and rate of maturing in Hereford and Angus cattle. *J. Anim. Sci.* 34: 525-537.

Brown, J.E., Fitzhugh, H.A. and T.C. Cartwright, 1976. A comparison of nonlinear models for describing weight-age relationships in cattle. *J. Anim. Sci.* 42: 810-818.

DeNise, R.S.K. and J.S. Brinks, 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. *J. Anim. Sci.* 61: 1431-1440.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Durbin, J. and G.S. Watson, 1951. Testing for serial correlation in least squares regression. II. *Biometrika* 38: 159-178.

Falconer, D.S., 1989. *Introduction to quantitative genetics.* 3rd ed. Longman Scientific & Technical Ltd. Harlow, England. 438 pp.

Fitzhugh, H.A., 1976. Analysis of growth curves and strategies for altering their shape. *J. Anim. Sci.* 42: 1036-1051.

Fitzhugh, H.A. and St.C.S. Taylor, 1971. Genetic analysis of degree of maturity. *J. Anim. Sci.* 33: 717-725.

Goonewardene, L.A., Berg, R.T. and R.T. Hardin, 1981. A growth study of beef cattle. *Can. J. Anim. Sci.* 61: 1041-1048.

Graser, H.U., Smith, S.P. and B. Tier, 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Anim. Sci.* 64: 1362-1370.

Gravir, K., 1967. Studies on different body measurements as estimators of live and carcass weight in young NRF bulls. *Acta Agric. Scand.* 17: 217-227.

Groen, A.F., 1989. Economic values in cattle breeding. I. Influences of production circumstances in situations without output limitations. *Livest. Prod. Sci.* 22: 1-16.

Groen, A.F. and H. Vos, 1995. Genetic parameters for body weight and growth in Dutch Black-and-White replacement stock. *Livest. Prod. Sci.* 41: 201-206.

Heinrichs, A.J., Rogers, G.W. and J.B. Cooper, 1992. Predicting body weight and wither height in Holstein heifers using body measurements. *J. Dairy Sci.* 75: 3576-3581.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 17-25.

Koops, W.J., 1986. Multiphasic growth curve analysis. *Growth* 50: 169-177.

Koops, W.J., 1989. *Multiphasic analysis of growth.* Ph.D. Thesis. Department of Animal Breeding, Wageningen Agricultural University. Wageningen, The Netherlands. 121 pp.

Lee, A.J., Boichard, D.A., McAllister, A.J., Lin, C.Y., Nadarajah, K., Batra, T.R., Roy, G.L. and J.A. Vesely, 1992. Genetics of growth, feed intake and milk yield in Holstein cattle. *J. Dairy Sci.* 75: 3145-3154.

Lin, C.Y., McAllister, A.J. and A.J. Lee, 1985. Multitrait estimation of relationships of first lactation yields to body weight changes in Holstein heifers. *J. Dairy Sci.* 68: 2954-2963.

Meijering, A. and A. Postma, 1985. Responses to sire selection for dystocia. *Livest. Prod. Sci.* 13: 251-266.

Meyer, K., 1985. Maximum likelihood estimation of variance components for a mixed model with equal design matrices. *Biometrics* 41: 153-165.

Meyer, K., 1991. *DFREML - a set of programs to estimate variance components by restricted maximum likelihood using a derivative-free algorithm.* User notes version 2.0. University New England. Armidale, Australia. 83 pp.

Perotto, D., Cue, R.I. and A.J. Lee, 1992. Comparison of nonlinear functions for describing the growth curve of three genotypes of dairy cattle. *Can. J. Anim. Sci.* 72: 773-782.

SAS®, 1990. *SAS Language: Reference. Version 6.* 1st ed. SAS Institute. Cary NC, USA. 1042 pp.

Silvey, M.W. and K.P. Haydock, 1978. A note on live-weight adjustment for pregnancy in cows. *Anim. Prod.* 27: 113-116.

Steverink, M.H.A., Groen, A.F. and P.B.M. Berentsen, 1994. The influence of environmental policies for dairy farms on dairy cattle breeding goals. *Livest. Prod. Sci.* 40: 251-261.

Steverink, M.H.A., Van Arendonk, J.A.M., Berentsen, P.B.M. and A.F. Groen, 1993. *Gecombineerde selectie op melkproduktiekenmerken en lichaamsgewicht.* Report Department of Animal Breeding, Wageningen Agricultural University. Wageningen, The Netherlands. 32 pp.

VanRaden, P.M., 1988. Economic value of body size in Holsteins. *J. Dairy Sci.* 72 (Suppl. 1): 1280.

Visscher, P.M., Bowman, P.J. and M.E. Goddard, 1994. Breeding objectives for pasture based dairy production systems. *Livest. Prod. Sci.* 40: 123-137.

CHAPTER 3

Phenotypic variation in live weight and live-weight changes of lactating Holstein-Friesian cows

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ABSTRACT

This study quantified individual phenotypic variation in live weight and live-weight changes during the first three lactations and estimated the effects of age, lactation week and pregnancy on live weight. Data comprised weekly averaged live weight (calculated from daily observations) during 452 lactations of 239 Holstein-Friesian cows. Unadjusted mean live weights were 553 (s.d. 50), 611 (s.d. 55) and 654 (s.d. 57) kg during first, second and third parity, respectively. Estimated effect of growth during parity was 46, 52 and 23 kg for the first three parities. Mean maximum weight loss was 26, 22 and 22 kg for first, second and third parity and variation was large among individuals. Week of lactation when cows had their maximum weight loss ranged from 7 weeks in first lactation to 13 weeks in third lactation. Estimated maximum effect of pregnancy on live weight during the lactation varied from 22 to 37 kg. Phenotypic variance in live weight increased with parity. Repeatabilities of live-weight observations within parity were 0.85. Across parities, high repeatabilities were found for calving weight and mean live weight but not for parameters associated with maximum weight loss. Correlations between weekly means and mean live weight during the whole of lactation were high. It was concluded that single live-weight observations of heifers are a good measurement of mean live weight during the first three parities.

INTRODUCTION

Maintenance requirements of dairy cattle largely depend on live weight (LW) (Agricultural Research Council, 1980). About 55% of the food cost of a cow from calving until fourth parity relates to maintenance requirements (Korver, 1988). Negative economic values have been reported for LW (e.g. Groen, 1989; Visscher *et al.*, 1994) because the costs associated with higher maintenance exceed revenues from selling culled animals with higher LW.

Mean LW might be a good measurement of the maintenance requirements during lactation. When interest is in mean LW, the predictive value of LW observations has to be known. Field studies on LW (e.g. Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995; Koenen and Groen, 1998) found a large phenotypic variance for LW. This variance is partly caused by three systematic effects: age dependent growth, lactation stage and pregnancy. First, cows gain weight until they reach maturity at approximately 5 years of age (Touchberry and Batra, 1976). Secondly, cows loose LW in early lactation as a result of negative energy balance. Later in lactation, LW increases when new tissue reserves are built up (Bines, 1976). Van Elzakker and Van Arendonk (1993) indicated that variation for LW changes during lactation was large among individuals. Thirdly, weight of the foetus, foetal membranes, uterus and uterus contents increase the LW of pregnant animals (Bereskin and Touchberry, 1967; Silvey and Haydock, 1978). When mean LW is predicted from field data of lactating cows adjustment for these systematic effects is needed.

Information on individual variation in LW changes during and across lactations and on adjustment factors for LW of lactating dairy cattle is limited. The correlation of single LW observations with mean LW and the repeatability of LW observations at different lactation stages and across parities determine the optimal moment and frequency of LW recording.

The aim of this study was to quantify phenotypic variation among individuals for LW and LW changes of Holstein-Friesian cows in the first three lactations.

MATERIAL AND METHODS

Data

Lactating Holstein-Friesian cows were weighed twice daily (directly after leaving the milking parlour) from January 1989 through August 1995 at the Institute for Animal Nutrition 'Schothorst' (Lelystad, The Netherlands). When LW was recorded for at least 4 days, weekly mean of LW was calculated and stored. Lactations with less than 35 weekly means or with missing values in the first three weeks of lactation were deleted. Only the first three parities were included in the analyses as the number of cows in higher parities was limited. The data included 18,875 weekly means for 239 cows in 452 lactations. The mean number of weekly means per animal during the first 45 weeks in lactation was 41 (s.d. 3). Missing values were replaced by estimated weekly means from fifth order polynomials, which were fitted for individual lactations. In the final data, 7% of the records were based on estimates.

The numbers of cows in first, second and third parity, were 185, 164 and 103, respectively. Mean, s.d. and range of unadjusted LW records for each parity are in Table 1. Out of the 185 heifers, 125 and 64 had also observations in second and third parity, respectively. Of the 103 third parity cows, 54 had also an observation at fourth calving.

Cows were given roughage *ad libitum* and a fixed amount of concentrates. Roughage consisted of fresh grass, grass silage, maize silage or a mixture of these roughages. Out of the 452 lactations, 217 were subject to four nutritional experiments. The amount of concentrates differed for each experiment. Every year in October a new experiment started with a different concentrate level and composition. Within each experiment, four to ten different levels of concentrates were included. All animals were in the same herd and were, apart from nutritional differences, subject to the same management.

Mean proportion of Holstein-Friesian genes of the animals was 0.93 (s.d. 0.09). Mean 305-day lactation milk yields were 7501, 9094 and 9663 kg in first, second and third parity, respectively.

Table 1. Number of cows, number of observations, mean, s.d., CV and range of unadjusted weekly averaged live weight in first, second and third parity.

	No. of cows	No. of obs.	Mean (kg)	s.d. (kg)	CV	Range (kg)
Parity 1	185	8325	553	50	0.09	410 – 711
Parity 2	164	7380	611	55	0.09	455 – 852
Parity 3	103	4635	654	57	0.09	496 – 869

To estimate the relationships between single observations and weekly means, bidaily LW observations from the experimental farm 'Ossenkampen' (Wageningen, The Netherlands) were used in addition to the main data. At this herd 5795 weights were collected on 70 Holstein-Friesian cows during 79 days. Weekly means were calculated in a similar procedure as in the first data set. After adjustment for parity, the correlation between single weighing and weekly means was estimated on decomposition of the intra-week variance.

Adjustment for fixed effects

Live-weight records from animal *l* calving in experimental group *i* and pregnancy group *k* were analysed by the following model:

$$y_{ijklm} = \mu + \mathrm{exp}_i + w_j + a_1 \times (age - \overline{\mathrm{age}}) + a_2 \times (age - \overline{\mathrm{age}})^2 + p_k + e_{ijklm}$$

where

y_{ijklm} = live weight (kg),
μ = intercept,
exp_i = fixed effect of the experimental group (27 levels),
w_j = fixed effect of lactation week (45 levels),
a_1, a_2 = regression coefficients,
age = age at calving (days),
p_k = fixed effect of pregnancy group (6 levels), and
e_{ijklm} = random error.

An experimental group was defined as a combination of experiment and treatment. All animals that were not included in an experiment were assigned to the same experimental group. Six classes for the effect of pregnancy were defined: ≤3, 4, 5, 6, 7 and ≥8 months pregnant. Stage of pregnancy was based on date of next calving, assuming a mean gestation length of 279 days. When date of next calving was not available, pregnancy stage was based on the time period since last insemination. Adjusted LW records were defined as $\mu + w_j + e_{ijklm}$.

Within each parity, the relative contribution of each fixed effect to the total variation in LW was calculated as the relative difference in mean square residual between the full model and models where one effect at a time was ignored. Fixed effects that were not significant were removed from the model.

Curve parameters

After adjusting the LW records, four new variables were defined to illustrate individual variation for LW during the lactation. Calving weight (CLW) was defined as LW at the first week of lactation. Mean live weight (MLW) was defined as mean LW during the first 45 weeks of lactation. Maximum weight loss (LOSS) was defined as CLW minus minimal LW during lactation. Week in lactation when LW was minimal was defined as MIN. Correlations between estimates for these variables were estimated within and across parities as a measure of the repeatability of LW and LW changes. Moreover, correlations between LW at different lactation weeks and MLW were estimated within and across parity.

RESULTS

Fixed effects

The proportion of variance explained by simultaneously considering experimental group, age at calving, week of lactation and pregnancy group ranged from 0.29 to 0.36 (Table 2). The largest proportion was explained by the effect of experimental group. The effect of age at calving decreased with parity and was no longer significant in third parity ($P > 0.05$).

Estimates for the effect of lactation week on LW during the first three lactations are in Figure 1. Live weight decreased after calving, was minimal at about five weeks and increased thereafter. Live weight clearly increased with parity. No significant effect was found for the effect of pregnancy in first lactation, whereas it was significant and small in the second and third parities. The estimated contrast between the first pregnancy group (≤3 months pregnant) and the sixth group (≥8 months pregnant) was 22 and 37 kg for second and third parity, respectively.

Table 2. Relative contribution of the fixed effects to the total phenotypic variance in live weight in first, second and third parity and the proportion of explained variance (R^2).

	First parity	Second parity	Third parity
Effect of			
Experiment	0.14	0.13	0.22
Week	0.04	0.12	0.03
Age	0.09	0.06	not significant
Pregnancy	not significant	0.00	0.00
R^2	0.34	0.36	0.29

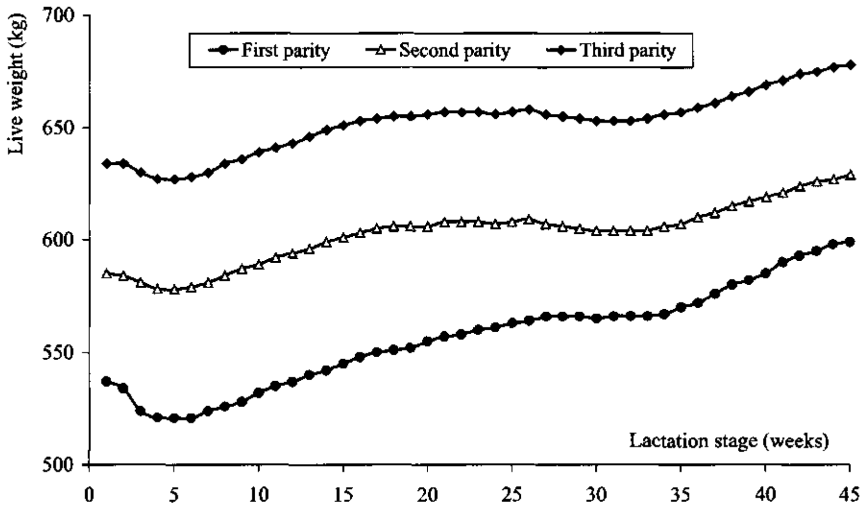

Figure 1. Effect of lactation stage on live weight in first, second and third parity.

Variance components and repeatabilities

Phenotypic variance in adjusted LW tended to be highest in the period 20 to 30 weeks of lactation and increased with parity (Table 3). Within all parities, correlations between adjusted LW observations were high and generally decreased with increasing time interval between repeated observations. This is illustrated for the first parity by the correlation matrix of LW (Table 3). The mean correlation between any pair of weekly means was 0.85, 0.84 and 0.85 in first, second and third parity, respectively. These means were estimated by averaging all possible combinations among the 45 weekly records and are a measurement of the repeatability.

Individual LW curves

Mean ± s.e., range and median of CLW, LOSS, MIN and MLW are in Table 4. The variables CLW and MLW increased with parity and reflected the effect of growth during first and second parity. The increase of MLW indicated a growth of 46 kg during first and 52 kg during second parity. Growth during third lactation was approximated as 23 kg by considering the mean LW of 656 kg at fourth calving of the 53 cows from the third parity group that had also an observation in he fourth parity. Mean values for LOSS and MIN characterised the shape of the LW curve. Mean LOSS in first, second and third parity was 26, 22 and 22 kg, respectively. Mean lactation week with minimum LW increased with parity: 7, 11 and 13 weeks in first, second and third parity, respectively.

Table 3. Phenotypic standard deviation (kg) of live weight in different weeks in the first three parities and correlations among repeated live weight observations in first parity after adjustment for fixed effects.

Lactation	Parity			Lactation week									
week	1	2	3	1	5	10	15	20	25	30	35	40	45
1	35.0	43.5	45.8	1.00	0.86	0.73	0.65	0.59	0.56	0.59	0.69	0.69	0.70
5	34.1	41.0	43.0		1.00	0.92	0.85	0.79	0.76	0.75	0.81	0.78	0.77
10	37.5	42.2	45.0			1.00	0.95	0.90	0.85	0.84	0.85	0.81	0.79
15	39.3	44.0	46.0				1.00	0.95	0.91	0.88	0.87	0.82	0.79
20	41.4	46.3	51.5					1.00	0.94	0.90	0.87	0.81	0.76
25	45.2	47.7	53.2						1.00	0.92	0.85	0.79	0.74
30	44.9	48.2	51.6							1.00	0.90	0.83	0.78
35	40.5	43.1	46.4								1.00	0.94	0.89
40	39.7	43.5	49.9									1.00	0.92
45	41.1	44.3	50.8										1.00

Table 4. Mean ± s.e., range and median of estimated calving weight (CLW), maximum weight loss (LOSS), lactation week with minimum live weight (MIN) and mean live weight (MLW) during lactation in first, second and third parity.

	Mean ± s.e.	Range	Median
First parity			
CLW (kg)	537 ± 35	458 – 636	536
LOSS (kg)	26 ± 20	0 – 94	23
MIN (weeks)	7 ± 5	1 – 28	5
MLW (kg)	557 ± 37	456 – 661	554
Second parity			
CLW (kg)	585 ± 43	487 – 763	581
LOSS (kg)	22 ± 23	0 – 137	16
MIN (weeks)	11 ± 12	1 – 40	6
MLW (kg)	603 ± 40	503 – 729	603
Third parity			
CLW (kg)	633 ± 46	532 – 781	636
LOSS (kg)	22 ± 25	0 – 107	13
MIN (weeks)	13 ± 11	1 – 39	9
MLW (kg)	655 ± 45	561 – 751	655

Table 5. Correlations between calving weight (CLW), maximum weight loss (LOSS), lactation week with minimum live weight (MIN) and mean live weight (MLW) during lactation in first, second and third parity.

Parameter	First parity	Second parity	Third parity
CLW – LOSS	0.37^{***}	0.46^{***}	0.34^{***}
CLW – MIN	0.19^{*}	0.17^{*}	0.29^{**}
CLW – MLW	0.74^{***}	0.75^{***}	0.78^{***}
LOSS – MIN	0.34^{***}	0.44^{***}	0.56^{***}
LOSS – MLW	-0.23^{**}	-0.12	-0.19
MIN – MLW	-0.16^{*}	-0.24^{**}	-0.19

Significance levels: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Variables derived from the LW curves had a large individual variation. Moreover, estimates for LOSS and MIN had a skewed distribution. Correlations among CLW, LOSS, MIN and MLW within each parity are in Table 5. Calving weight was highly correlated with MLW (0.74 to 0.78). Calving weight had a moderate positive correlation (0.34 to 0.46) with LOSS and with MIN (0.17 to 0.29).

Table 6. Correlations across parities for calving weight (CLW), maximum weight loss (LOSS), lactation stage with minimum live weight (MIN) and mean live weight (MLW) (number of animals within brackets).

	First – second (n = 125)	First – third (n = 64)	Second – third (n = 87)
CLW	0.53^{***}	0.56^{***}	0.61^{***}
LOSS	0.12	0.10	0.52^{***}
MIN	0.18	0.16	0.14
MLW	0.76^{***}	0.76^{***}	0.82^{***}

Significance level: *** $P < 0.001$.

Table 7. Correlation between live weight at different lactation stages and mean live weight during the first 305 days of lactation.

Week	First parity	Second parity	Third parity
1	0.74	0.75	0.78
5	0.89	0.88	0.87
10	0.95	0.94	0.93
15	0.96	0.95	0.94
20	0.95	0.94	0.94
25	0.93	0.92	0.94
30	0.93	0.93	0.95
35	0.95	0.94	0.94
40	0.92	0.90	0.91
45	0.88	0.89	0.89

Correlations of the same trait across parities were high for CLW and MLW, whereas they were low for MIN and MWL (Table 6). Based on the within and between animal variation, the repeatability for CLW, LOSS, MIN and MLW were 0.54, 0.22, 0.12 and 0.75, respectively.

Weekly means for LW across the lactation were highly correlated with MLW (Table 7): correlations were highest between 10 and 35 weeks in lactation. The correlations between weekly LW in first parity and MLW in first, second and third parity depended on lactation week and were on average 0.92, 0.70 and 0.71, respectively. Correlation between single weighings and weekly means, based on the records of the additional data, was 0.95.

DISCUSSION

Statistical analysis

The aim of this study was to quantify individual variation for LW and LW changes. Parameters were derived from adjusted phenotypic records on LW. In other studies, models with biologically interpretable parameters such as the Wood function (Wood, 1967) were used. The Wood function explained only a small part of the variation for LW (Wood *et al.*, 1980; Berglund and Danell, 1987). Moreover, problems with systematic bias, especially in early lactation, might be expected (Cobby and Le Du, 1978).

Repeated observations can also be analysed using random regression models or covariance functions. These models describe individual variation in the shape of a curve and are also able to account for heterogeneity of variance across the curve during lactation (e.g. Schaeffer and Dekkers, 1994; Andersen and Pedersen, 1996). When a random regression model using orthogonal polynomials was used in the present study and the log likelihood ratio test was used to test the significance of higher order polynomials, a high order polynomial was needed to describe LW data (results not shown). These techniques would have been more valuable if observations were only available at a low frequency and interest was in describing variance for lactation stages without observations (Kirkpatrick and Heckman, 1989).

Fixed effects

Adjustment factors were estimated from the data. Experimental group explained a large proportion of variance. This might be due to variation in nutrition but also due to variation caused by season of calving as the start of an experiment was largely confounded with season of calving. Results from field data (Hietanen and Ojala, 1995; Koenen and Groen, 1998) showed a large variation between herds for LW.

In this study, the mean lactation stage with minimum weight increased with parity, whereas no systematic trend for the maximum weight loss was found. Berglund and Danell (1987) found an increased weight loss with increased parity: weight loss increased from 13 kg at 45 days in first parity to 17 kg at 60 days in third parity. Hohenbroken *et al.* (1995) found a negative relationship between rearing intensity and lactation stage with MLW and MIN. Korver *et al.* (1985) found for higher parity Holstein-Friesian cows on a concentrate diet a mean weight loss of over 50 kg at 88 days in lactation.

Estimated effects of parity on LW are in line with results of Miller *et al.* (1969) and Touchberry and Batra (1976) on Holstein-Friesian cows. The parity effects in this study could have been biased upwards as a result of selection for milk yield since positive correlations between LW and yield have been reported (Ahlborn and Dempfle, 1992). This hypothesis was tested by selecting those 124 heifers that had the opportunity to complete three lactations. Out of this group, 63 had records during all three lactations. When MLW means during lactation of these cows were compared with heifers that were culled before third lactation no significant difference for unadjusted LW was found, indicating that the bias in this study is minimal.

Estimates for the effect of pregnancy varied widely between parities and were hard to predict. One of the problems in estimating the effect of parity could have been a confounding of days in lactation and days pregnant, especially in first parity cows. However, when age at calving was removed from the model for first parity cows, a contrast of around 50 kg was estimated. Based on field data, Koenen and Groen (1998) estimated an effect of 28 kg when ≥8 months pregnant. Results from Bereskin and Touchberry (1967) indicated a weight of around 40 kg. Silvey and Haydock (1978) suggested that adjustment of LW data of lactating cattle for pregnancy stage is only needed in late lactation and in the dry period.

Variance components and correlations

Observations of weekly means in different weeks had a high repeatability. Repeatabilities of single weights are expected to be lower than repeatabilities of weekly means. But the estimated high correlation between single weights and weekly means (0.95) implied that the correlation between single weighings and MLW is also high.

The high phenotypic correlations for MLW across parities are in agreement with results of Oldenbroek (1984) and Persuad *et al.* (1991). These correlations and the high repeatabilities within and across parities for most lactation weeks indicate that LW observations on heifers are suitable to predict MLW, not only during the first but also during the second and third lactation.

CONCLUSION

After adjustment for age at calving, experimental group and pregnancy stage, LW observations are highly repeatable within and across parities. Live-weight observations during lactation were highly correlated with estimated lactation MLW. It was concluded that single LW observations of heifers are a good measurement of LW during the first three parities.

REFERENCES

Agricultural Research Council, 1980. *The nutrient requirements of ruminant livestock.* Commonwealth Agricultural Bureaux. Slough, England. 351 pp.

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Andersen, S. and B. Pedersen, 1996. Growth and food intake curves for group-housed gilts and castrated male pigs. *Anim. Sci.* 63: 457-464.

Bereskin, B. and R.W. Touchberry, 1967. Some effects of pregnancy on body weight and paunch girth. *J. Dairy Sci.* 50: 220-224.

Berglund, B. and B. Danell, 1987. Live weight changes, feed consumption, milk yield and energy balance in dairy cattle during the first period of lactation. *Acta Agric. Scand.* 37: 495-509.

Bines, J.A., 1976. Regulation of food intake in dairy cows in relation to milk production. *Livest. Prod. Sci.* 3: 115-128.

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

Groen, A.F., 1989. Economic values in cattle breeding. I. Influences of production circumstances in situations without output limitations. *Livest. Prod. Sci.* 22: 1-16.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 17-25.

Hohenbroken, W.D., Foldager, J., Jensen, J., Madsen, P. and B. Bech Andersen, 1995. Breed and nutritional effects and interactions on energy intake, production and efficiency of nutrient utilization in young bulls, heifers and lactating cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 92-98.

Kirkpatrick, M. and N. Heckman, 1989. A quantitative genetic model for growth, shape, reaction norms and other infinite dimensional characters. *J. Math. Biol.* 27: 429-450.

Koenen, E.P.C. and A.F. Groen, 1998. Genetic evaluation of body weight of lactating Holstein heifers using body measurements and conformation traits. *J. Dairy Sci.* 81: 1709-1713.

Korver, S., 1988. Genetic aspects of feed intake and feed efficiency in dairy cattle. *Livest. Prod. Sci.* 20: 1-13.

Korver, S., Van Arendonk, J.A.M. and W.J. Koops, 1985. A function for live-weight change between two calvings in dairy cattle. *Anim. Prod.* 40: 233-241.

Miller, R.H., Hooven Jr., N.W. and M.E. Creegan, 1969. Weight changes in lactating Holstein cows. *J. Dairy Sci.* 52: 90-94.

Oldenbroek, J.K., 1984. Holstein Friesians, Dutch Friesians and Dutch Red and Whites on two complete diets with a different amount of roughage: differences in performance between first and second lactation. *Livest. Prod. Sci.* 11: 417-428.

Persuad, P., Simm, G. and W.G. Hill, 1991. Genetic and phenotypic parameters for yield, food intake and efficiency of dairy cows fed ad libitum. 1. Estimates for 'total' lactation measures and their relationship with live-weight traits. *Anim. Prod.* 52: 435-444.

Schaeffer, L.R. and J.C.M. Dekkers, 1994. Random regressions in animal models for test-day production in dairy cattle. *Proc. 5th World Congr. Gen. Appl. Livest. Prod.* 18: 443-446.

Silvey, M.W. and K.P. Haydock, 1978. A note on the live-weight adjustment for pregnancy in cows. *Anim. Prod.* 27: 113-116.

Touchberry, R.W. and T.R. Batra, 1976. Body weight changes in lactating purebred and crossbred dairy cattle. *J. Dairy Sci.* 59: 733-743.

Van Elzakker, P.J.M. and J.A.M. Van Arendonk, 1993. Feed intake, body weight and milk production: genetic analysis of different measurements in lactating dairy heifers. *Livest. Prod. Sci.* 37: 37-51.

Visscher, P.M., Bowman, P.J. and M.E. Goddard, 1994. Breeding objectives for pasture based dairy production systems. *Livest. Prod. Sci.* 40: 123-137.

Wood, P.D.P., 1967. Algebraic model of the lactation curve in cattle. *Nature* 216: 164-165.

Wood, P.D.P., King, J.O.L. and P.G. Youdan, 1980. Relationships between size, live-weight change and milk production characters in early lactation in dairy cattle. *Anim. Prod.* 31: 143-151.

CHAPTER 4

Genetic evaluation of body weight of lactating Holstein heifers using body measurements and conformation traits

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ABSTRACT

Genetic and phenotypic parameters of body weight (BW), hip height, heart girth and linear conformation traits were estimated from field data of 7344 lactating Holstein heifers from 560 herds. Mean BW was around 540 kg at calving, decreased to a minimum of 514 kg in week 6 and increased to >580 kg at the end of lactation. The statistical model for BW included month of recording, lactation stage, pregnancy stage, proportion of Holstein genes, parity of the dam, calving age, herd and animal. Variation between herds accounted for 33% of the phenotypic variation of BW. Estimated heritability was 0.33 for BW and ranged from 0.32 to 0.54 for heart girth, hip height and conformation traits. Genetic correlations of BW with heart girth, hip height, body depth, rump width and muscularity ranged from 0.43 to 0.77. The accuracy of a selection index was 0.90 for direct selection and 0.83 for indirect selection using information on those conformation traits of 50 daughters. Genetic variation of BW is considerable and genetic evaluation of BW can be based on data for conformation traits from a field recording system with only a limited loss of accuracy.

INTRODUCTION

In dairy cattle, body weight (BW) has a negative economic value (Dempfle, 1989; Groen, 1989; Visscher *et al.*, 1994). Inclusion of BW in an aggregate genotype or breeding goal is only effective in terms of changing genetic trends when BW measurements on potential breeding animals or their relatives are also in the information index (Groen and Korver, 1990). Currently BW is not included in most breeding schemes for dairy cattle. To include BW in such a breeding scheme, a suitable method of recording has to be available. Weighing animals on a large scale is not common practice. Therefore, traits that are already included in a regular recording scheme, such as body measurements or conformation traits, might be used as predictors of BW (Heinrichs *et al.*, 1992; Veerkamp and Brotherstone, 1997). Moreover, for a genetic evaluation, appropriate genetic and phenotypic parameters of BW have to be known. Reported heritabilities of BW for Holstein cattle were moderate to high and were mostly based on data from single experimental herds during limited lactation periods (Van Elzakker and Van Arendonk, 1993; Veerkamp and Brotherstone, 1997). Heritability estimates for BW from field data are scarce. Ahlborn and Dempfle (1992) analysed subjective scoring of BW of heifers and found a heritability of 0.24. Hietanen and Ojala (1995) estimated BW using heart girth measurements and found a heritability of 0.13 for heifers. At present, knowledge is limited about field recording of BW and about genetic and phenotypic parameters of BW.

This study estimated genetic and phenotypic parameters of BW of field data and studied possibilities for genetic evaluation of BW using observations on body measurements and linear conformation traits.

MATERIALS AND METHODS

Data

From September 1995 through March 1996 BW, heart girth, hip height and linear conformation traits were collected for 7344 lactating Holstein heifers from 560 herds; the number of heifers per herd ranged from 3 to 65. Conformation traits were linearly scored by eight classifiers of the Royal Dutch Cattle Syndicate and BW and heart girth were measured by seven persons specifically trained for this experiment. Scores for body depth, rump width, muscularity and udder depth ranged from 1 to 9 and size and dairy character scores ranged from 65 to 100 (Table 1). For each trait, heifers were evaluated only once. In the final data, observations for each conformation trait were standardised to an equal standard deviation within classifiers to account for differences in variation between classifiers. Observations on body depth, rump width, muscularity and udder depth were adjusted to a standard deviation of 1.50 points; observations on size and dairy character were adjusted to a standard deviation of 4.00 points. Age at calving was on average 795 days (s.d. 75) and ranged from 522 to 1090 days. Mean stage of lactation stage at measurement was 129 days (s.d. 82). Mean 305-day lactation production records for milk, fat and protein were 7113, 312 and 247 kg, respectively.

Table 1. Unadjusted phenotypic mean, s.d. and range for body weight, body measurements and conformation traits (n = 7344).

Trait	Mean	s.d.	Range
Body weight (kg)	546	56.5	373 – 855
Heart girth (cm)	192.9	7.34	166 – 222
Hip height (cm)	141.7	3.72	126 – 157
Body depth[1]	5.23	1.57	1 – 9
Rump width[1]	4.87	1.50	1 – 9
Muscularity[1]	4.71	1.67	1 – 9
Udder depth[1]	4.76	1.36	1 – 9
Size[2]	80.9	4.30	65 – 89
Dairy character[2]	80.5	3.71	65 – 92

[1] Scales: body depth (1 = shallow to 9 = deep), rump width (1 = narrow to 9 = wide), muscularity (1 = poor to 9 = strong) and udder depth (1 = deep to 9 = shallow).

[2] Scores ranged from 65 to 100.

Statistical analysis

Observations on BW, heart girth, hip height and linear conformation traits were described by the following models:

$$\begin{aligned}
\mathrm{BW}_{ijklmno} &= \mathrm{mo}_i + \mathrm{lac}_j + \mathrm{preg}_k + \mathrm{hf}_l + \mathrm{pari}_m + \mathrm{a} \times \mathrm{age} + \mathrm{h}_n + \mathrm{ani}_o + \mathrm{e}_{ijklmno} \\
\mathrm{HG}_{ijklmpno} &= \mathrm{mo}_i + \mathrm{lac}_j + \mathrm{preg}_k + \mathrm{hf}_l + \mathrm{pari}_m + \mathrm{pers}_p + \mathrm{a} \times \mathrm{age} + \mathrm{h}_n + \mathrm{ani}_o + \mathrm{e}_{ijklmpno} \\
\mathrm{HT}_{ilqmno} &= \mathrm{mo}_i + \mathrm{hf}_l + \mathrm{clas}_q + \mathrm{pari}_m + \mathrm{a} \times \mathrm{age} + \mathrm{h}_n + \mathrm{ani}_o + \mathrm{e}_{ilqmno} \\
\mathrm{CT}_{ijlqno} &= \mathrm{mo}_i + \mathrm{lac}_j + \mathrm{hf}_l + \mathrm{clas}_q + \mathrm{a} \times \mathrm{age} + \mathrm{h}_n + \mathrm{ani}_o + \mathrm{e}_{ijlqno}
\end{aligned}$$

where

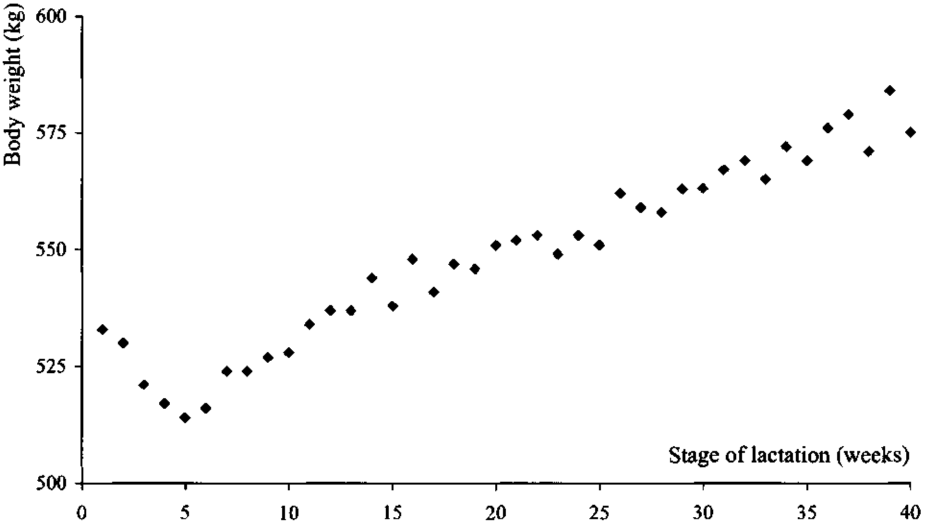
$\mathrm{BW}_{ijklmno}$ = body weight (kg),
$\mathrm{HG}_{ijklmpno}$ = heart girth (cm),
HT_{ilqmno} = hip height (cm),
CT_{ijlqno} = conformation trait,
mo_i = fixed effect of month of scoring (7 levels),
lac_j = fixed effect of lactation stage (21 levels),
preg_k = fixed effect of stage of pregnancy (6 levels),
hf_l = fixed effect of the genetic group (4 levels),
pari_m = fixed effect of parity of the dam (2 levels),
pers_p = fixed effect of person (7 levels),
clas_q = fixed effect of classifier (8 levels),
a = regression coefficient,
age = age at calving (days),
h_n = random effect of herd (560 levels),
ani_o = random effect of animal (7344 levels), and
$\mathrm{e}_{ijklmno}$ = random residual term.

Four genetic groups were defined according to percentage of Holstein genes (≤62.5, 75, 87.5 and 100%). Grouping did not account only for additive effects but also might have corrected for possible heterosis effects and recombination losses. Seven months of scoring were used: September through March. Lactation stage was defined in the model as 21 biweekly periods: week 1 to 2, week 3 to 4, ..., week 39 to 40 and week ≥41. Stage of pregnancy was divided into six groups: ≤3 months, 4 months, ..., 7 months and ≥8 months pregnant. Effect of pregnancy on BW was expected to be minimal during the first three months of calving (Bereskin and Touchberry, 1967). Two parity classes were defined: parity 1 or parity ≥2 of the dam. Significance ($P < 0.05$) of the fixed effects in each model was tested by the MIXED procedure of SAS® (1990). To account for genetic relationships, a matrix of additive genetic relationships including parents and grandparents of the heifer was included. The 736 bulls included in the data sired on average 9.6 daughters; the number of daughters per sire ranged from 1 to 1463. Estimates for the variance components were obtained by a REML method using a derivative-free algorithm (Meyer, 1991). Genetic and phenotypic correlations among traits were estimated from bivariate analyses using starting values for the variances from the univariate analyses. Restarts using the estimates were used to test if a global maximum was found for the –2×log(likelihood). Standard errors of genetic correlations were approximated according to methods of Falconer (1989). Accuracy of selection for BW in a field-recording scheme was evaluated by comparing selection indexes including direct or indirect measurements of BW for different progeny group sizes.

RESULTS

To illustrate the change of BW during lactation, unadjusted means for phenotypic observations are presented on a weekly basis in Figure 1. Number of observations in a week ranged from 22 to 296. Mean BW at calving was around 535 to 540 kg, decreased to a minimum of 514 kg in week 6 and increased to >580 kg at the end of the lactation. The estimated regression coefficient of BW on age at calving was 0.21 kg/day. The BW of heifers having a multiparous dam was about 11 kg higher than that of heifers having a primiparous dam. Estimates for the effect of pregnancy on BW ranged from 2.1 kg when heifers were four months pregnant to 28 kg when eight months pregnant or more. Estimates for the effect of the proportion of Holstein genes were 0, –1.23, –1.09 and –0.73 kg for the classes ≤62.5, 75, 87.5 and 100% Holstein, respectively.

Figure 1. Mean unadjusted body weight of heifers during lactation.



Heritability estimates for BW, heart girth and hip height were 0.33, 0.33 and 0.54, respectively (Table 2). Heritabilities of linear conformation traits ranged from 0.32 to 0.52. Relative herd variance was moderate for BW (0.33) and heart girth (0.21) but low for other traits (0.06 to 0.12).

Table 2. Estimated additive genetic variance (σ^2_a), herd variance (σ^2_c), error variance (σ^2_e), relative herd variance (c^2) and heritability (h^2) of body weight, body measurements and linear conformation traits.

Trait	σ^2_a	σ^2_c	σ^2_e	c^2	h^2
Body weight	813.7	828.4	850.5	0.33	0.33[1]
Heart girth	14.11	8.86	19.3	0.21	0.33
Hip height	7.11	1.63	4.41	0.12	0.54
Body depth	0.906	0.129	1.05	0.06	0.43
Rump width	0.713	0.177	1.36	0.08	0.32
Muscularity	0.994	0.186	1.09	0.08	0.44
Udder depth	0.784	0.203	1.27	0.09	0.35
Size	8.03	1.77	5.61	0.12	0.52
Dairy character	6.86	1.18	7.26	0.08	0.45

[1] Estimated s.e. of the heritabilities ranged from 0.04 to 0.07.

Table 3. Genetic (below diagonal) and phenotypic correlations (above diagonal) between body weight, body measurements and linear conformation traits.

Trait[1]	BW	HG	HT	BD	RW	MU	UD	SI	DC
BW		0.74	0.46	0.42	0.19	0.54	–0.15	0.49	0.11
HG	0.77[2]		0.46	0.40	0.20	0.44	–0.09	0.48	0.08
HT	0.50	0.51		0.35	0.28	0.07	0.13	0.95	0.51
BD	0.48	0.44	0.33		0.27	0.25	–0.28	0.47	0.38
RW	0.43	0.35	0.38	0.43		0.04	–0.11	0.31	0.19
MU	0.58	0.31	–0.15	0.08	0.16		–0.08	0.10	–0.25
UD	–0.18	–0.02	0.32	–0.49	–0.26	–0.15		0.07	–0.01
SI	0.59	0.60	0.95	0.49	0.45	–0.10	0.16		0.61
DC	0.15	0.14	0.65	0.56	0.25	–0.47	–0.01	0.70	

[1] BW = body weight, HG = heart girth, HT = hip height, BD = body depth, RW = rump width, MU = muscularity, UD = udder depth, SI = size and DC = dairy character.

[2] Estimated s.e. of the genetic correlations ranged from 0.01 to 0.11.

Table 4. Accuracy of selection for three alternative selection indexes for body weight based on 10, 25, 50, 100 and 200 effective daughters.

Index traits	n = 10	n = 25	n = 50	n = 100	n = 200
BW[1]	0.69	0.83	0.90	0.95	0.97
HT + BD + RW + MU	0.62	0.74	0.79	0.83	0.85
HT + BD + RW + MU + HG	0.65	0.77	0.83	0.87	0.89

[1] BW = body weight, HT = hip height, BD = body depth, RW = rump width, MU = muscularity and HG = heart girth.

Genetic correlations among BW, heart girth, hip height and conformation traits are in Table 3. Heart girth has the highest genetic correlation with BW ($r = 0.77$). Genetic correlations of BW with hip height, body depth, rump width, muscularity and size were 0.50, 0.48, 0.43, 0.58 and 0.59, respectively. Hip height and size had a high genetic correlation ($r = 0.95$).

The accuracy of a selection index based on 50 effective daughters was 0.90 for direct BW measurements and 0.79 when observations on hip height, body depth, rump width and muscularity were used (Table 4). These conformation traits are presently included in the regular scoring system in the Netherlands, but BW and heart girth are not. When information on heart girth was added, the accuracy of selection increased to 0.83.

DISCUSSION

Mean BW of heifers in our study was 546 kg and was much larger than the mean BW of 356 kg of Holstein heifers in New Zealand (Ahlborn and Dempfle, 1992) and the mean BW of 473 kg in Finland (Hietanen and Ojala, 1995). Mean BW in our study is in line with results from North America. Hoffman (1997) reviewed seven studies of Holstein replacement heifers and found a mean postpartum (day 0 to 7) BW of 559 kg and a mean BW of 532 kg at 30 days postpartum.

The effect of lactation was modelled using fixed effect classes i.e. shape of the BW curve as a function of time was assumed to be equal for all heifers. Maltz *et al.* (1991) found different BW curves for low and high producing heifers. To evaluate the effect of production on BW heifers with the 25% lowest (<6319 kg) and the 25% highest (>7861 kg) 305-day yield were compared. Mean unadjusted BW of low producing heifers was significantly ($P < 0.01$) lower than of high producing heifers (533 *vs.* 561 kg). However, after adjustment for the mean group effect, estimates for the stage of lactation did not differ between the groups ($P > 0.05$).

Holstein heifers in this study originated from an upgraded Dutch-Friesian population. Variation in BW between different genetic groups might exist as the Holstein is a more dairy-oriented breed than the Dutch Friesian (Oldenbroek, 1980). No systematic trend was found for BW when the proportion of Holstein genes increased. However, hip height and scores for body depth, size and dairy character increased as Holstein proportion increased, but scores for muscularity decreased. The increase in BW as a correlated response by increased height, body depth, size and dairy character seemed to be compensated by decreased muscularity of the Holstein breed (Oldenbroek, 1980).

The relative effect of a multiparous dam on BW of around 2% (11 kg) that was found in this study was in line with an increase of 1.5% for BW at calving found by Koenen and Groen (1996). For BW at birth, an increase of 5 to 10% from first to later parity has been reported (Meijering and Postma, 1985; Kertz *et al.*, 1997). Variation between herds accounted for 33% of the total phenotypic variation of BW, which was in agreement with an estimate of 35% of Hietanen and Ojala (1995). This variation might be due to variation in nutrition and management during the rearing period and variation in the time period between weighing and the last milking of the heifers.

When heritability estimates of this study are compared with literature values, it should be noted that herd was treated as a random effect in the model. When data were reanalysed treating herd as a fixed effect, estimates for additive and error variance were close to the original estimates. However, heritability estimates increased with herds treated as fixed, especially when herd variance was large. The heritability estimate of BW in this study was considerable higher than other estimates based on field data using indirect measurements (Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995), but were, in most cases, lower than in studies based on actual weights of single herds (Van Elzakker and Van Arendonk, 1993; Veerkamp and Brotherstone, 1997). Estimated heritabilities for conformation traits were in line with earlier estimates of the Dutch Friesian (Luijkx *et al.*, 1992).

In this study, parameters for heifer BW were estimated; in earlier studies on breeding goals, mostly mature BW was considered (Groen, 1989). However, high genetic and phenotypic correlations have been found between BW observations at different ages (Persuad *et al.*, 1991; Koenen and Groen, 1996), suggesting that heifer BW is a proper information source for the breeding goal mature weight.

To evaluate the effect of inclusion of BW in the breeding goal on genetic responses, genetic relations with other traits such as milk production, feed intake and body condition scores have to be considered simultaneously. Genetic correlations of BW with production traits were generally reported to be positive and low (Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995) and to depend on lactation stage (Miller *et al.*, 1973; Van Elzakker and Van Arendonk, 1993).

Positive correlations between BW and body condition score (Wildman *et al.*, 1982; Veerkamp and Brotherstone, 1997) suggest that selection for a decreased BW might result in an unfavourable decrease in body condition score. Because body condition is independent of frame size (Wildman *et al.*, 1982), the correlated response in body condition score might be minimal when genetic evaluation for BW is based on traits related to skeletal measurements such as height, rump width and body depth. Incorporation of measures of skeletal growth when defining body size was also suggested by Hoffman (1997) as BW *per se* might not be an appropriate measure of size.

CONCLUSIONS

The BW of heifers has considerable genetic and phenotypic variation. Routine genetic evaluation of BW can be based on indirect measurements such as conformation traits rather than on direct measurement of BW with only a limited loss of accuracy.

REFERENCES

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Bereskin, B. and R.W. Touchberry, 1967. Some effects of pregnancy on body weight and paunch girth. *J. Dairy Sci.* 50: 220-224.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Groen, A.F., 1989. Economic values in cattle breeding. I. Influences of production circumstances in situations without output limitations. *Livest. Prod. Sci.* 22: 1-16.

Groen, A.F. and S. Korver, 1990. Feed intake capacity of lactating cows in dairy and dual purpose cattle selection. *J. Anim. Breed. Genet.* 107: 389-396.

Falconer, D.S., 1989. *Introduction to quantitative genetics.* 3rd ed. Longman Scientific & Technical Ltd. Harlow, England. 438 pp.

Heinrichs, A.J., Rogers, G.W. and J.B. Cooper, 1992. Predicting body weight and wither height in Holstein heifers using body measurements. *J. Dairy Sci.* 75: 3576-3581.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 17-25.

Hoffman, P.C., 1997. Optimum body size of Holstein replacement heifers. *J. Anim. Sci.* 75: 836-845.

Kertz, A.F., Reutzel, L.F., Barton, B.A. and R.L. Ely, 1997. Body weight, body condition score and whither height of prepartum Holstein cows and birth weight and sex of calves by parity: a database and summary. *J. Dairy Sci.* 80: 525-529.

Koenen, E.P.C. and A.F. Groen, 1996. Genetic analysis of growth patterns of Black-and-White dairy heifers. *J. Dairy Sci.* 79: 495-501.

Luijkx, R., Van der Werf, J.H.J. and A. Van der Lugt, 1992. *Estimation of parameters and prediction of functional herd life, based on type traits.* Department of Animal Breeding, Wageningen Agricultural University. Wageningen, The Netherlands. 25 pp.

Maltz, E., Kroll, O., Spahr, S.L., Devir, S., Genizi, A. and R. Sagi, 1991. Milk yield, parity and cow potential as variables for computerized concentrate supplementation strategy. *J. Dairy Sci.* 74: 2277-2289.

Meijering, A. and A. Postma, 1985. Responses to sire selection for dystocia. *Livest. Prod. Sci.* 13: 251-266.

Meyer, K., 1991. *DFREML - a set of programs to estimate variance components by restricted maximum likelihood using a derivative-free algorithm.* User notes version 2.0. University New England. Armidale, Australia. 83 pp.

Miller, R.H., Hooven Jr., N.W., Smith J.W. and M.E. Creegan, 1973. Usefulness of periodic body weights to predict yield, intake and feed efficiency of lactating cows. *J. Dairy Sci.* 56: 1540-1545.

Oldenbroek, J.K., 1980. Breed and crossbreeding effects in a crossing experiment between Dutch Friesian and Holstein Friesian cattle. *Livest. Prod. Sci.* 7: 235-241.

Persuad, P., Simm, G. and W.G. Hill, 1991. Genetic and phenotypic parameters for yield, food intake and efficiency of dairy cows fed ad libitum. 1. Estimates for 'total' lactation measures and their relationship with live-weight traits. *Anim. Prod.* 52: 435-444.

SAS®, 1990. *Language: Reference* Version 6. 1st ed. SAS Institute. Cary NC, USA. 1042 pp.

Van Elzakker, P.J.M. and J.A.M. Van Arendonk, 1993. Feed intake, body weight and milk production: genetic analysis of different measurements in lactating dairy heifers. *Livest. Prod. Sci.* 37: 37-51.

Veerkamp, R.F. and S. Brotherstone, 1997. Genetic correlations between linear type traits, food intake, live weight and condition score in Holstein Friesian dairy cattle. *Anim. Sci.* 64: 385-392.

Visscher, P.M., Bowman, P.J. and M.E. Goddard, 1994. Breeding objectives for pasture based dairy production systems. *Livest. Prod. Sci.* 40: 123-137.

Wildman, E.E., Jones, G.M., Wagner, P.E., Boman, R.L., Troutt Jr., H.F. and T.N. Lesch, 1982. A dairy cow body condition scoring system and its relationship to selected production characteristics. *J. Dairy Sci.* 65: 495-501.

CHAPTER 5

Genetic covariance functions for live weight, condition score and dry-matter intake measured at different lactation stages of Holstein-Friesian heifers

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ABSTRACT

Genetic parameters for live weight, condition score and dry-matter intake of dairy heifers were estimated using covariance function methodology. Data were from 469 heifers of the Langhill Dairy Cattle Research Centre and included observations during the first 25 weeks of lactation. Genetic variances for live weight and condition score were estimated by a second order polynomial covariance function, whereas the genetic variance for dry-matter intake was described by a third order polynomial covariance function. Heritability estimates for observations measured at different stages of lactation ranged from 0.43 to 0.56 for live weight, from 0.21 to 0.45 for condition score and from 0.18 to 0.37 for dry-matter intake. Genetic correlations between repeated observations for live weight and condition score were large (0.84 to 1.00). For dry-matter intake, observations in early lactation had a low to moderate genetic correlation to observations in mid-lactation.

INTRODUCTION

Live weight (LW), condition score (CS) and dry-matter intake (DMI) of dairy cattle have been discussed as traits that might be of interest for genetic selection (e.g. Dempfle, 1989; Steverink *et al.*, 1994; Veerkamp, 1998). These traits are influenced by different biological processes that can change during the course of the lactation (e.g. Bines, 1976; Journet and Remond, 1976). Therefore these traits might have a different genetic background at different lactation stages. Estimates for the genetic variation at different lactation stages and the genetic inter-relationships are needed to decide on optimal frequency and moment of recording, optimal selection strategies and for the evaluation of selection response. Genetic analyses of lactating heifers showed moderate to high heritabilities for LW, CS and DMI (review in Veerkamp, 1998). Most estimates for genetic variances, however, originate from small experiments and have therefore large sampling errors. For this reason, methods that can use the available data in a more efficient way are desired.

As an alternative to pooling repeated records on the same animal, a repeatability model might be used. In a repeatability model, the genetic variance is described by only one variance component, but this is only justified when genetic variances are independent of lactation stage and genetic correlations between lactation stages equal unity. These assumptions might not be valid for all lactation stages. Alternatively, a multi-trait analysis estimates genetic variation for each lactation stage separately and estimates genetic covariances between each pair of lactation stages. This means that in the case of observations at n different lactation stages, $n(n+1)/2$ (co)variance components are needed to describe the genetic variation. Estimating many highly correlated parameters is computationally demanding and results in estimates with low accuracies that might reduce the accuracy of selection (references in Veerkamp and Goddard, 1998).

Kirkpatrick and Heckman (1989) suggested the use of covariance functions (CFs) to estimate variance components from longitudinal data. A genetic CF describes the covariance between breeding values at any two lactation stages as a function of lactation stage and might be preferred over multivariate analyses. First, CFs often need less parameters to describe genetic covariances compared to multi-trait analyses. Secondly, the amount of information used to estimate the covariances is used in a more efficient way as a CF considers the ordering and spacing of repeated observations. Thirdly, unlike a multi-trait analysis, a CF can describe genetic variation at intermediate lactation stages where no observations are available. Fourthly, an estimated CF might provide a more accurate evaluation of the genetic variance at the range of lactation stages considered (Kirkpatrick and Heckman, 1989).

The aim of this study was to estimate genetic parameters for LW, CS and DMI of dairy heifers using CF methodology.

MATERIAL AND METHODS

Data

Data from 469 Holstein-Friesian heifers were collected at the Scottish Agricultural College / University of Edinburgh Langhill Dairy Cattle Research Centre in the period August 1982 through July 1996. Heifers calved between August and January and were kept indoors in a conventional cubicle housing system from calving to July. Individual data were recorded for a period of 26 weeks. Starting at calving, heifers were weighed and their body condition was scored once a week. Condition scores were based on the scoring system of Lowman *et al.* (1976), with units ranging from 0 (lean) to 5 (fat) with increments of 0.25. Observations on DMI were available from week 3 of lactation onwards; they were obtained by recording food offered and refused on four consecutive days in a week. Missing records (<5% of the data) were estimated using polynomial regression (Veerkamp *et al.*, 1994). The experiment comprised two genetic lines: a selection (S) and a control (C) line. In total 74 sires were used: the number of offspring per sire ranged from 1 to 22. Selection of sires was based on their predicted transmitting abilities (PTA) for production. Selection line animals were bred to sires with the highest genetic merit for kg fat and protein, whereas the C animals were bred to sires of about national average genetic merit for fat and protein. The average PTA-index for C heifers (n = 184) was -5.99 kg (s.d. 5.3), whereas it was 25.90 kg (s.d. 9.9) for S heifers (n = 285). From September 1988 onwards, heifers of both genetic lines were randomly allocated to a high (HC) or a low (LC) concentrate feeding system. Feed was offered *ad libitum* as a complete mixed diet, with proportions (in total DM) of concentrates, brewer's grains and silage of either

20:5:75 (LC; 1.0 tonne concentrates per annum) or 45:5:50 (HC; 2.5 tonne concentrates per annum). The number of heifers in the four line by diet combination groups was 188, 97, 118 and 66 for S-HC, S-LC, C-HC and C-LC, respectively. For the final analyses, the data file contained observations on LW and CS at calving and observations on LW, CS and DMI at 3, 5, 10, 15, 20 and 25 weeks of lactation.

Statistical model

Observations in lactation stage *i* on animal *l* of group *k* calved in season *j* were described by the following animal model:

$$y_{ijkl} = s_{ij} + l_{ik} + b_i \times \text{age} + a_{il} + e_{ijkl}$$

where

y_{ijkl} = observation (LW, CS or DMI) for animal *l* at lactation stage *i*,
s_{ij} = fixed effect of season of calving (2 levels),
l_{ik} = fixed effect of line by diet by year interaction (44 levels),
b_i = linear regression coefficient,
age = age at calving (days),
a_{il} = random animal effect (469 levels), and
e_{ijkl} = random residual term.

Fixed effects were estimated for each lactation stage separately. Two seasons of calving were defined: the first group heifers calved in the period August through October, the second group in November through January. Year was included to account for increasing differences between the genetic lines. Pregnancy started on average at 117 days (s.d. 51) in lactation. However, the effect of days pregnant as a linear, quadratic and cubic regression on LW, CS and DMI was not significant ($P > 0.05$). Random effects were assumed normally distributed with var(a) = **G** and var(e) = **R**. In estimating the additive genetic variance, a genetic relationship matrix with pedigree traced back six generations was included in the analyses (n = 1771 animals).

Covariance functions

The additive genetic CFs for each trait were fitted following the model suggested by Kirkpatrick *et al.* (1990). This means that covariances are described by orthogonal polynomials, which are a function of lactation stage. A genetic covariance structure of observations at *n* lactation stages can be fitted by an *n*th order polynomial CF (full fit) which is equivalent to a multi-trait analysis. The genetic covariance between observations at x_l and x_m weeks in lactation on the same animals is then described as:

$$\mathrm{Cov}(x_l, x_m) = \sum_{i=0}^{p-1}\sum_{j=0}^{p-1} \phi_i(x_l)\,\phi_j(x_m)\,\mathrm{k}_{ij}$$

where ϕ_i is the ith polynomial for a pth order of fit and x is standardised lactation stage ($-1 \leq x \leq 1$). k_{ij} are the coefficients of matrix **K** and represent the coefficients of the CF. Standardisation of lactation stages (0, 3, 5, 10, 15, 20 and 25 weeks) was needed as Legendre polynomials are only defined in the range –1 to 1. This was done by defining x_{min} and x_{max} as the first and last time point on the trajectory considered. Lactation stage a_i was then transformed to x_i by $x_i = 2(a_i - a_{min})/(a_{max} - a_{min}) - 1$. In matrix notation the additive genetic CF can be written as $\mathbf{G} = \mathbf{\Phi}\,\mathbf{K}\,\mathbf{\Phi}'$, where **G** is the additive genetic covariance matrix of order n for breeding values at n given lactation stages and $\mathbf{\Phi}$ is a $n \times p$ matrix with orthogonal polynomials. Coefficient matrix **K** was estimated using a Restricted Maximum Likelihood algorithm (Meyer and Hill, 1997). A CF including a lower order polynomial, i.e. $p < n$ (reduced fit) for the additive genetic variance might describe the data statistically consistent with a full order fit but requires less parameters to be estimated. After estimating a first order polynomial CF for the additive genetic variance, the order of the polynomial function was stepwise increased until a full fit was reached. The order of the final model was chosen as the lowest order that did not decrease the likelihood significantly ($P < 0.05$) compared to a full fit. The likelihood of two nested models were compared using the test statistic (TS) = –2 × the difference between their logarithmic likelihoods. Under the null hypothesis, TS is asymptotically distributed as a χ^2-distribution with m degrees of freedom where m is the difference in the number of estimated covariance parameters (Wilks, 1938).

Estimates for the variance components from the CFs were compared with multi-trait analyses considering repeated observations for each trait as observations on different traits. For these analyses canonical transformations (Thompson and Hill, 1990) were used to reduce computational demands.

Eigenfunctions and eigenvalues

Eigenfunctions and eigenvalues can also be used to analyse patterns of genetic variation during a time period. Eigenfunctions are a function of the lactation stages and can be interpreted as a continuous equivalent of eigenvectors from a covariance matrix of a multi-trait analysis. Eigenfunctions and eigenvalues describe major patterns of variation. The eigenfunctions of the additive genetic covariance function associated with the largest eigenvalues identify potential changes for which the population has substantial genetic variation (Kirkpatrick *et al.*, 1994).

The eigenfunction $\psi_i(x)$ was constructed from the relation:

$$\psi_i(x) = \sum_{j=0}^{p-1} [\mathrm{k}_{\psi i}]_j \phi_j(x)$$

where $[\mathrm{k}_{\psi i}]_j$ is the jth element of the ith eigenvector of **K**. An eigenvalue is associated with each eigenfunction and is proportional to the amount of genetic variation in the population corresponding to that eigenfunction. Eigenvalues λ_i were obtained by singular value decomposition of matrix **K** (Kirkpatrick *et al.*, 1990). The number of eigenfunctions and eigenvalues equals the order of fit and eigenfunctions and eigenvalues were derived from both the full and reduced fit.

RESULTS

Means and standard deviations for LW, CS and DMI are in Table 1. Mean LW increased from 532 kg at calving to 568 kg at week 25 of lactation. Mean CS decreased from 2.67 units at calving to 2.49 units at week 25, the unadjusted phenotypic standard deviation of CS increased from 0.21 units at calving to 0.48 units at week 25 of lactation. Mean DMI increased from 13.0 kg/day in week 3 to 15.5 kg/day at week 15 and decreased hereafter until 14.5 kg/day at week 25.

For DMI and LW the coefficients of variation appear unaffected by lactation stage, but for CS the coefficient of variation increases with increasing lactation stage from 0.08 to 0.19.

Table 1. Unadjusted mean and standard deviation of live weight (LW), condition score (CS) and dry-matter intake (DMI) in different lactation weeks (n = 469 heifers).

	LW (kg)		CS (units)		DMI (kg/day)	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
Week 0	532	47	2.67	0.21	n.a.[1]	n.a.
Week 3	520	46	2.65	0.23	13.0	2.3
Week 5	523	45	2.62	0.22	14.1	2.2
Week 10	537	48	2.54	0.27	15.4	2.5
Week 15	550	50	2.51	0.34	15.5	2.7
Week 20	560	53	2.49	0.42	14.9	2.6
Week 25	568	56	2.49	0.48	14.5	2.6

[1] n.a. = not available.

Estimates for the genetic variances of the CFs are compared with estimates of the multi-trait estimates in Figures 1-3. Estimates and their associated likelihoods for the full fit CFs were very close the multi-trait results (not shown). Small discrepancies might be related to convergence problems due to the high dimension of the derivative-free search (Meyer and Hill, 1997). The multi-trait estimates for the genetic variation for LW during lactation increased from 571 kg^2 at calving to 1551 kg^2 at week 25 (Figure 1). For LW, the likelihood-ratio test showed that the likelihood of a third order CF was not different from a second order CF (TS = 7.4; $\chi^2_{0.05,\ df\ =\ 3} = 7.81$). However, estimates from the second order CF were systematically lower than the multi-trait estimates at many lactation stages. The multi-trait estimates for the genetic variance of CS increased from 0.0072 $units^2$ at calving to 0.0816 $units^2$ at 25 weeks in lactation (Figure 2). The likelihood-ratio test showed that the second order CF was statistically consistent with the data.

For DMI, the genetic variance increased from 0.49 $(kg/day)^2$ at week 3 to 1.40 $(kg/day)^2$ at week 15 and decreased hereafter to 0.88 $(kg/day)^2$ at week 25 (Figure 3). A third order CF was selected by the likelihood-ratio test.

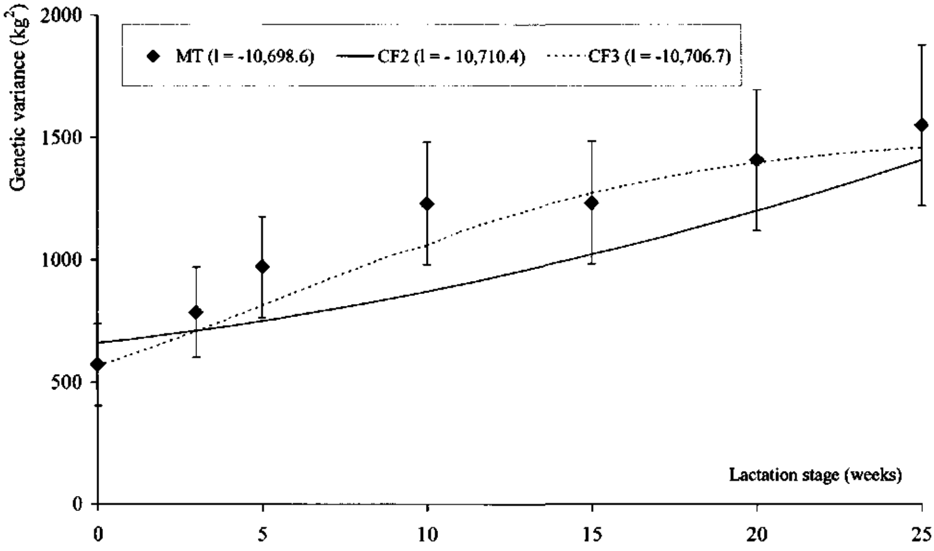

Figure 1. Genetic variance of live weight during first lactation estimated by multi-trait analysis (MT, including s.e.), a second order covariance function (CF2) and a third order covariance function (CF3) and their associated likelihoods (l).

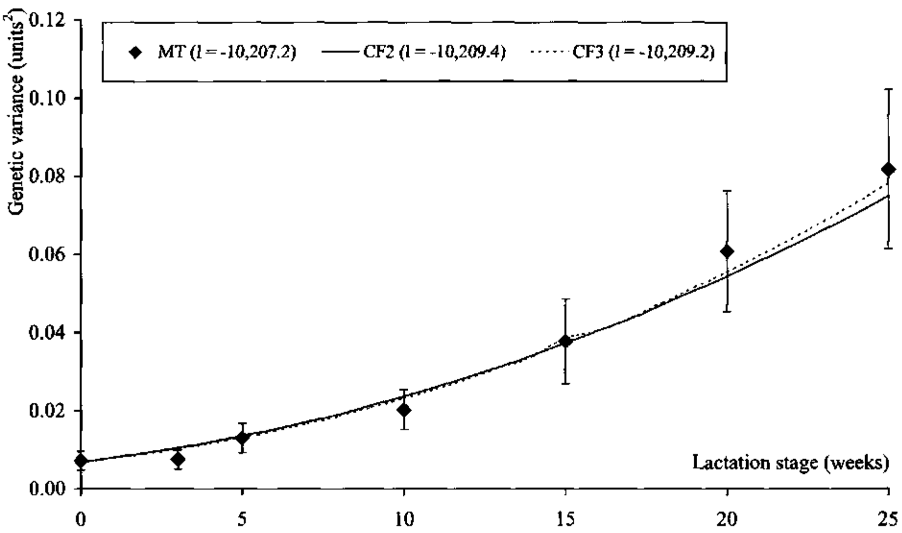

Figure 2. Genetic variance of condition score during first lactation estimated by multi-trait analysis (MT, including s.e.), a second order covariance function (CF2) and a third order covariance function (CF3) and their associated likelihoods (l).

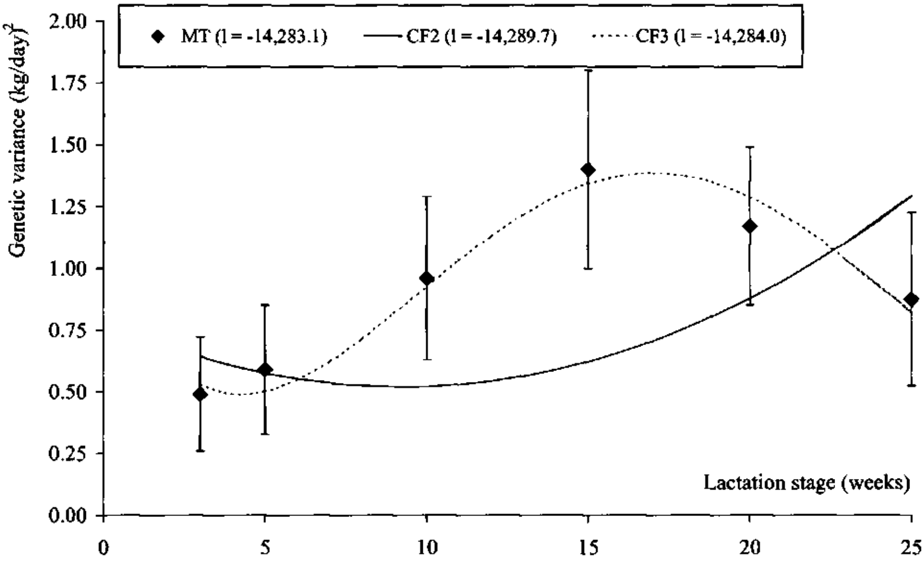

Figure 3. Genetic variance of dry-matter intake during first lactation estimated by multi-trait analysis (MT, including s.e.), a second order covariance function (CF2) and a third order covariance function (CF3) and their associated likelihoods (l).

The covariances between observations at x_l and x_m on LW, CS and DMI were described by $\mathrm{Cov}(x_l, x_m) = 943.0 + 187.4\ (x_l + x_m) + 91.7\ x_l x_m$ (kg^2), $\mathrm{Cov}(x_l, x_m) = 0.0301 + 0.0170\ (x_l + x_m) + 0.0108\ x_l x_m$ (units^2) and $\mathrm{Cov}(x_l, x_m) = 1.289 + 0.343\ (x_l + x_m) + 0.386\ x_l x_m - 0.749\ (x_l^2 + x_m^2) - 0.269\ x_l(x_l^2 + x_l x_m) + 0.499\ x_l^2 x_m^2$ (kg/day)^2, respectively. Based on these CFs heritabilities, genetic and error correlations for LW, CS and DMI were estimated. For LW, heritability estimates ranged from 0.43 to 0.56 and increased with lactation stage (Table 2). Genetic correlations between LW observations at different lactation stages were high (0.88 to 1.00). Heritabilities of CS ranged from 0.21 to 0.45 (Table 3). Observations for CS at different lactation stages had a high genetic correlation (0.84 to 1.00). Heritabilities for DMI ranged from 0.18 to 0.37 and were highest at week 15 and week 20 (Table 4). Genetic correlations between DMI observations in early and mid-lactation clearly deviated from unity.

For all traits, error terms were clearly correlated and decreased when the time period between lactation stages increased (Tables 2-4).

Based on the full fit, the two main eigenfunctions for LW and CS accounted for 99.7 and 99.1% of the total variation, respectively. For DMI, the three main eigenfunctions accounted for 99.7% the total variation. For all traits, the reduced fit was able to describe the data statistically consistent with the results of the full fit and emphasis is on the main eigenfunctions of the reduced fits. Eigenvalues based on the reduced fit ($p = 2$) approximated the eigenvalues of the full fit.

Estimated eigenfunctions and their associated eigenvalues of the reduced CFs are in Table 5. Considering the reduced fit, the first eigenfunction of LW represents 98% of the genetic variation (1911 as a proportion of the sum of the two eigenvalues), whereas the second eigenfunction represents the remaining 2%.

Table 2. Heritabilities (diagonal), genetic correlations (above diagonal) and error correlations (below diagonal) for live weight at different lactation stages based on a second order polynomial covariance function.

	Week 0	Week 3	Week 5	Week 10	Week 15	Week 20	Week 25
Week 0	**0.43**[1]	1.00	0.99	0.97	0.94	0.91	0.88
Week 3	0.64	**0.43**	1.00	0.99	0.97	0.94	0.92
Week 5	0.62	0.77	**0.48**	0.99	0.98	0.96	0.94
Week 10	0.43	0.62	0.83	**0.48**	1.00	0.99	0.97
Week 15	0.34	0.51	0.74	0.86	**0.50**	1.00	0.99
Week 20	0.27	0.47	0.67	0.81	0.89	**0.54**	0.99
Week 25	0.22	0.41	0.63	0.74	0.83	0.88	**0.56**

[1] Approximated s.e. of the heritabilities ranged from 0.06 to 0.10.

Table 3. Heritabilities (diagonal), genetic correlations (above diagonal) and error correlations (below diagonal) for condition score at different lactation stages based on a second order polynomial covariance function.

	Week 0	Week 3	Week 5	Week 10	Week 15	Week 20	Week 25
Week 0	**0.21**[1]	0.99	0.97	0.92	0.89	0.86	0.84
Week 3	0.63	**0.24**	1.00	0.98	0.96	0.94	0.92
Week 5	0.62	0.57	**0.35**	0.99	0.98	0.96	0.95
Week 10	0.36	0.27	0.51	**0.38**	1.00	0.99	0.98
Week 15	0.22	0.09	0.33	0.69	**0.40**	1.00	1.00
Week 20	0.16	0.03	0.20	0.50	0.79	**0.42**	1.00
Week 25	0.12	0.02	0.15	0.42	0.67	0.80	**0.45**

[1] Approximated s.e. of the heritabilities ranged from 0.06 to 0.10.

Table 4. Heritabilities (diagonal), genetic correlations (above diagonal) and error correlations (below diagonal) for dry-matter intake at different lactation stages based on a third order polynomial covariance function.

	Week 3	Week 5	Week 10	Week 15	Week 20	Week 25
Week 3	**0.18**[1]	0.90	0.45	0.20	0.04	−0.14
Week 5	0.53	**0.19**	0.79	0.60	0.45	0.25
Week 10	0.37	0.50	**0.29**	0.96	0.90	0.74
Week 15	0.31	0.35	0.46	**0.37**	0.98	0.88
Week 20	0.31	0.35	0.36	0.47	**0.35**	0.95
Week 25	0.22	0.24	0.35	0.31	0.52	**0.21**

[1] Approximated s.e. of the heritabilities ranged from 0.06 to 0.10.

Table 5. Estimated eigenfunctions ($\psi(x)$) and their associated eigenvalues (λ) for live weight, condition score and dry-matter intake.

Live weight	$\psi_1(x)$[1] $= 0.702 + 0.142\,x$	$\lambda_1 = 1911$
	$\psi_2(x) = -0.082 + 1.216\,x$	$\lambda_2 = 36$
Condition score	$\psi_1(x) = 0.671 + 0.384\,x$	$\lambda_1 = 666$
	$\psi_2(x) = -0.222 + 1.163\,x$	$\lambda_2 = 7$
Dry-matter intake	$\psi_1(x) = -0.839 - 0.234\,x + 0.481\,x^2$	$\lambda_1 = 18{,}224$
	$\psi_2(x) = -0.059 + 1.186\,x - 0.286\,x^2$	$\lambda_2 = 2029$
	$\psi_3(x) = -0.646 + 0.196\,x - 2.305\,x^2$	$\lambda_3 = 116$

[1] x: lactation stage (weeks) scaled to range −1 to 1.

The two main eigenfunctions based on the full and reduced fit are illustrated in Figure 4. The first eigenfunction has positive values throughout the period from 0 to 25 weeks. This implies that the main principal component of variation has positive weightings for LW at all lactation stages, e.g. a breeding value for LW at calving is highly correlated with breeding values at all other lactation stages. Only a minor part of the variation (2%) is related to the eigenfunction that has a trade-off between early and mid lactation. For CS the results were comparable, the first and second eigenfunction explained 99 and 1% of the genetic variation, respectively. For DMI the first eigenfunction accounted for 85% of the variation and had positive values throughout the recording period. The second eigenfunction, accounting for 10% of the variation, was associated with a trade-off between breeding values in early lactation and mid-lactation. The third eigenfunction accounted for 1% of the variation and described a combination of variance that had relatively high weightings on breeding values at week 0 and 25 but not on breeding values at the intermediate lactation stages.

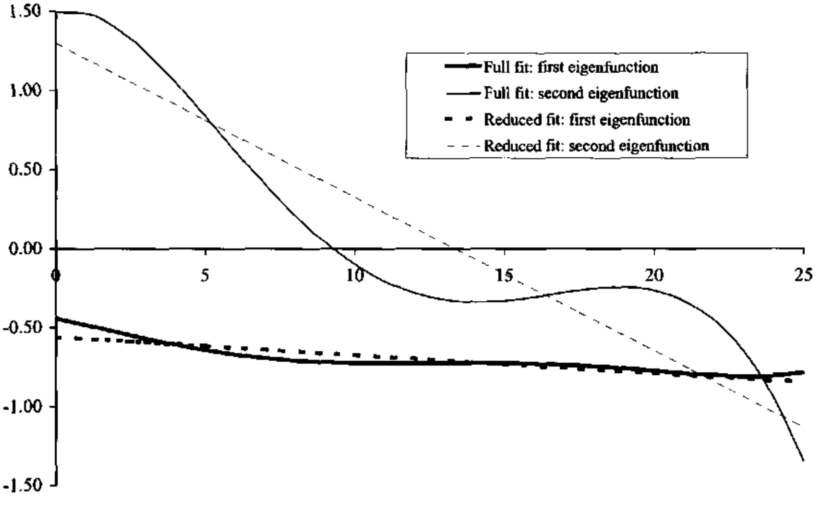

Figure 4. Estimates of the first two eigenfunctions based on the full and reduced fit of additive genetic variation for live weight during the first 25 weeks of lactation.

DISCUSSION

Covariance functions

The aim of this study was to estimate genetic covariances for LW, CS and DMI observations of dairy heifers during early and mid-lactation using CFs. As the true function of the variance is unknown, the variance during lactation was approximated by orthogonal polynomial functions. In this study, the likelihood ratio test was used to test the significance of nested models and to select the order of the polynomials of the final models. However, recent work (Stram and Lee, 1994) indicated that the distribution of the test statistic might be biased when the tested parameter vector lies at the boundary of the parameter space. Therefore, the different models were also compared using the Akaikes Information Criterion (Akaike, 1973) as an informal test. This test confirmed the order of fit for the final models. For LW, the likelihood ratio test favoured a second order CF. However, the additive variance was systematically underestimated at many lactation stages, compared with estimates from the multi-trait analysis. It is unlikely that this discrepancy is due to sampling errors in the multi-trait estimates (Figure 1). This implies that when testing the appropriate order of fit of an model, analysis of the discrepancies between multi-trait and CF estimates during the whole time-period is also important. It might be that the choice of function is important. Following Kirkpatrick *et al.* (1994) and Meyer and Hill (1997) Legendre polynomials were used in this study. This might have affected the estimated variance components and further investigations might include the use of functions other than the Legendre polynomials. Considering the selected lactation stages as single traits resulted in overparameterisation. For the multi-trait analysis, 28 or 21 parameters were needed to describe the genetic variance, whereas only three (LW, CS) or six parameters (DMI) were needed when CFs were used. This reduction in parameters, whilst accounting for the fact that records are ordered in time, is a main advantage of CFs and should result in a more accurate selection (Veerkamp and Goddard, 1998).

In this study, the error variance was fitted as a full fit model, which yields, at points in time where there are measurements, the same variances as a multi-trait model. The number of parameters to describe the error variance could have been reduced further when the error variation was described as a combination of a CF for the environmental effect and a measurement error effect for days where records are available (Kirkpatrick *et al.*, 1994). This model has the advantage that correlations between two measurements at the same day are not assumed to be unity. Ignoring this effect in the present analysis affects covariances for days close together: these are likely to be towards unity. As the emphasis was on estimating CFs for the genetic variance, this approach has not been further pursued herein. In this study, a multi-trait analysis at a limited number of lactation stages was compared with a CF analysis at the same lactation stages. A further improvement on the method used herein, is to include measurements at all lactation stages when fitting the CF. Meyer and Hill (1997) indicated that observations at all lactation stages can be used by a random regression approach (Schaeffer and Dekkers, 1994), and similarity between the two approaches has been illustrated recently (Meyer, 1998).

Genetic parameters

Although sampling errors might have been smoothed by the use of CFs, parameter estimates still have a large sampling error as they are based on a small number of animals. Therefore, these estimates should be interpreted carefully, and be compared to results in other studies. Moreover, the *ad libitum* feeding of a total mixed ration in this experiment should also be considered when the results are compared to field data. For example, practical feeding regimes might not have allowed such a large increase in variation of LW and CS during lactation.

Estimated heritabilities for LW were in line with other studies from single herd data (Lin *et al.,* 1985; Lee *et al.*, 1992; Jensen *et al.*, 1995; Koenen and Groen, 1996) but were higher than heritability estimates of around 0.30 for field data (Ahlborn and Dempfle, 1992; Koenen and Groen, 1998). Estimates for the genetic parameters of CS of dairy cattle are scarce. Heritabilities reported for beef cattle (Johnston *et al.,* 1996) ranged from 0.14 to 0.21 and were lower than estimates in this study. Heritability estimates for DMI are in line with other studies (Van Arendonk *et al.*, 1991; Van Elzakker and Van Arendonk, 1993; Svendsen *et al.*, 1994; Jensen *et al.*, 1991). In an earlier analysis of the present data, Veerkamp and Brotherstone (1997) pooled all observations during the first 26 weeks of lactation and analysed individual means. Heritabilities were 0.55, 0.43 and 0.43 for LW, CS and DMI, respectively.

High genetic correlations among repeated observations were found for LW and CS. Also Svendsen *et al.* (1994) found high genetic correlations between LW observations at different lactation stages. As genetic correlations are close to unity, a repeatability model with lactation stage as a fixed effect might be an adequate approximation. However, adjustments for heterogeneous variance might be needed when breeding value estimation for LW and CS is based on field data recorded at different lactation stages.

Genetic correlations for DMI clearly decreased with increased time period between lactation stages. In an earlier study of the Langhill experiment, Persuad and Simm (1991) studied mean DMI of 6-week periods in a group of heifers and higher parity cows. They found a genetic correlation of 0.56 between mean DMI during week 3 to 8 and mean DMI during week 21 to 26. A genetic correlation of energy intake in week 2 and week 9 of 0.47 has been reported when heifers were fed roughage *ad libitum* and a fixed amount of concentrates (Van Elzakker and Van Arendonk, 1993). If correlations between early and later stages of lactation are significantly lower than unity, there are implications for the selection strategy. Observations for DMI in late lactation have then lower predictive value when the aim is to improve DMI in early lactation. On the other hand, when the objective is to improve DMI over the whole lactation, measurements might be needed throughout all lactation stages. Observed DMI is expected to be genetically related to other traits such as milk production and feed intake capacity. These relations might change with increasing lactation stage. Positive genetic correlations between milk yield and DMI (e.g. Jensen *et al.*, 1995; Veerkamp and Brotherstone, 1997) would suggest that selection for milk yield increases DMI automatically. However, several studies (e.g. Hooven *et al.*, 1972; Brandt *et al.*, 1985; Gravert, 1985; Korver, 1988) showed that the genetic relation between feed intake and production was lower in early than in late lactation. Koenen and Veerkamp (1997) found that in early lactation, selection line heifers mobilised more body tissues than control line heifers to meet energy requirements.

When information on LW, CS and DMI are to be used in a breeding scheme, additional information is required about the relationships between these traits and other traits in the breeding goal such as milk production.

REFERENCES

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Akaike, H., 1973. *Information theory and an extension of the maximum likelihood principle.* Pages 267-281 *in*: Petrov, B.N. and F. Csáki (Eds.). 2nd Intern. Symp. on Information Theory. Akadémiai Kiadó. Budapest, Hungary.

Bines, J.A., 1976. Regulation of food intake in dairy cows in relation to milk production. *Livest. Prod. Sci.* 3: 115-128.

Brandt, A., Papst, K., Schulte-Coerne, H. and H.O. Gravert, 1985. Die Heritabilität der Futteraufnahme bei Milchkühen. *Züchtungsk.* 57: 299-308.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research Bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Gravert, H.O., 1985. Genetic factors controlling feed efficiency in dairy cows. *Livest. Prod. Sci.* 13: 87-99.

Hooven, N.W., Miller, R.H. and J.W. Smith, 1972. Relationships among whole- and part lactation, gross feed efficiency, feed consumption and milk yield. *J. Dairy Sci.* 55: 1113-1122.

Jensen, J., Hohenbroken, W.D., Madsen, P. and B.B. Andersen, 1995. Sire × nutrition interaction and genetic parameters for energy intake, production and efficiency of nutrient utilization in young bulls, heifers and lactating cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 81-91.

Johnston, D.J., Chandler, H. and H.U. Graser, 1996. Genetic parameters for cow weight and condition score in Angus, Hereford and Polled Hereford cattle. *Aust. J. Agric. Res.* 47: 1251-1260.

Journet, M. and B. Remond, 1976. Physiological factors affecting the voluntary intake of feed by cows: a review. *Livest. Prod. Sci.* 3: 129-146.

Kirkpatrick, M. and N. Heckman, 1989. A quantitative genetic model for growth, shape, reaction norms and other infinite-dimensional characters. *J. Math. Biol.* 27: 429-450.

Kirkpatrick, M., Hill, W.G. and R. Thompson, 1994. Estimating the covariance structure of traits during growth and ageing, illustrated with lactation in dairy cattle. *Genet. Res.*

Camb. 64: 57-69.

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

Koenen, E.P.C. and A.F. Groen, 1996. Genetic analysis of growth patterns of Black-and-White heifers. *J. Dairy Sci.* 79: 495-501.

Koenen, E.P.C. and A.F. Groen, 1998. Genetic evaluation of body weight of lactating Holstein heifers using body measurements and conformation traits. *J. Dairy Sci.* 81: 1709-1713.

Koenen, E.P.C. and R.F. Veerkamp, 1997. *Genotype by diet interactions for live-weight and condition score during lactation in heifers.* Page 38 *in*: Proc. Br. Soc. Anim. Sci. Scarbourough, England.

Korver, S. 1988. Genetic aspects of feed intake and feed efficiency in dairy cattle: a review. *Livest. Prod. Sci.* 20: 1-13.

Lee, A.J., Boichard, D.A., McAllister, A.J., Lin, C.Y., Nadarajah, K., Batra, T.R., Roy, G.L. and J.A. Vesely, 1992. Genetics of growth, feed intake and milk yield in Holstein cattle. *J. Dairy Sci.* 75: 3145-3154.

Lin, C.Y., McAllister, A.J. and A.J. Lee, 1985. Multitrait estimation of relationships of first lactation yields to body weight changes in Holstein heifers. *J. Dairy Sci.* 68: 2954-2963.

Lowman, B.G., Scott, N.A. and S.H. Somerville, 1976. *Condition scoring of cattle.* Rev. ed. Bull. 6. The East of Scotland College of Agriculture. Edinburgh, Scotland. 31 pp.

Meyer, K., 1998. Modelling 'repeated' records: covariance functions and random regression models to analyse animal breeding data. *Proc. 6th World Congr. Genet. Appl. Livest. Prod.* 25: 517-520.

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

Persuad, P. and G. Simm, 1991. Genetic and phenotypic parameters for yield, food intake and efficiency of dairy cows fed ad libitum. 2. Estimates for part lactation measures and their relationship with 'total' lactation measures. *Anim. Prod.* 52: 445-450.

Schaeffer, L.R. and J.C.M. Dekkers, 1994. Random regressions in animal models for test-day production in dairy cattle. *Proc. 5th World Congr. Genet. Appl. Livest. Prod.* 18: 443-446.

Steverink, M.H.A., Groen, A.F. and P.B.M. Berentsen, 1994. The influence of environmental policies for dairy farms on dairy cattle breeding goals. *Livest. Prod. Sci.* 40: 251-261.

Stram, D.O. and J.W. Lee, 1994. Variance components testing in the longitudinal mixed effects model. *Biometrics* 50: 1171-1177.

Svendsen, M., Skipeness, P. and I.L. Mao, 1994. Genetic correlations in the feed conversion complex of primiparous cows at a recommended and a reduced plane of nutrition. *J. Anim. Sci.* 72: 1441-1449.

Thompson, R. and W.G. Hill, 1990. Univariate REML analyses for multivariate data with the animal model. *Proc. 4th World Congr. Genet. Appl. Livest. Prod.* 13: 484-487.

Van Arendonk, J.A.M., Nieuwhof, G.J., Vos, H. and S. Korver, 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. *Livest. Prod. Sci.* 29: 263-275.

Van Elzakker, P.J.M. and J.A.M. Van Arendonk, 1993. Feed intake, body weight and milk production: genetic analysis of different measurements in lactating dairy heifers. *Livest.*

Prod. Sci. 37: 37-51.

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. and S. Brotherstone, 1997. Genetic correlations between linear type traits, food intake, live weight and condition score in Holstein Friesian dairy cattle. *Anim. Sci.* 64: 385-392.

Veerkamp, R.F. and M. Goddard, 1998. Covariance functions across herd production levels for test day records on milk, fat and protein yields. *J. Dairy Sci.* 81: 1690-1701.

Veerkamp, R.F., Simm, G. and J.D. Oldham, 1994. Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows. *Livest. Prod. Sci.* 39: 229-241.

Wilks, S.S., 1938. The large-sample distribution of the likelihood ratio for testing composite hypothesis. *Ann. Math. Stat.* 9: 60-62.

CHAPTER 6

Relationships between body weight, body measurements and milk yield in Holstein heifers

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ABSTRACT

Five size traits (body weight, heart girth, hip height, body depth and rump width) and three milk production traits (milk, fat and protein) of 7192 heifers were analysed on a monthly and 305-day lactation basis. Genetic parameters were estimated by multi-trait analyses and covariance function methodology. The additive genetic variation was moderate to high and changed over time. Genetic correlations between observations for size traits measured in different months were high. Genetic correlations between size traits and 305-day lactation yields ranged from –0.14 to 0.26. This study did not indicate that these correlations were time-dependent.

INTRODUCTION

Traits that describe the size of a dairy cow include body weight, heart girth, hip height, body depth and rump width. Size traits are positively related to maintenance requirements (Agricultural Research Council, 1980) and have a considerable genetic variation (Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995; Koenen and Groen, 1998). Dempfle (1989) suggested a negative weighting on body weight and a positive weighting on yield when making selection decisions. When combining these traits, estimates for the genetic interrelations between size and milk production needed. Estimated genetic correlations between body weight and milk, fat and protein yields are generally low, ranging from around zero (Lee *et al.*, 1992; Hietanen and Ojala, 1995) to around 0.35 (Ahlborn and Dempfle, 1992). Genetic correlations between linear type and production traits are low to moderate (Misztal *et al.*, 1992; Brotherstone, 1994).

Most studies considered observations at different lactation stages as observations on the same trait and assumed a constant genetic relation between size traits and yield during lactation. The genetic variance for body weight might change over time (Koenen and Veerkamp, 1998). Analysing the data at different lactation weeks, Van Elzakker and Van Arendonk (1993) found that the genetic correlation between body weight and milk production changed from 0.29 in week 3 to –0.25 in week 13, whereas other studies (e.g. Maltz *et al.*, 1991; Koenen and Veerkamp, 1997) suggested that dairy heifers selected for high production had different body-weight change patterns during lactation than non-selected heifers.

Many studies used multi-trait analyses for the estimation of covariances. When many different parameters have to be estimated, the accuracy of each estimate will be very low, especially when the number of observations is low. New statistical techniques such as covariance function (CF) methodology (Kirkpatrick *et al.*, 1990) and random regression models (Schaeffer and Dekkers, 1994) might describe continuous patterns of variation data more efficiently.

The aim of this study was to estimate the dynamics of genetic parameters for body weight, body measurements and milk production during first lactation using multi-trait and CF methodology.

MATERIAL AND METHODS

Data

Observations on body weight, heart girth, hip height, body depth and rump width within the first 305 days of lactation of 7192 Holstein-Friesian heifers in 560 Dutch herds were collected in a field experiment (Koenen and Groen, 1998). Observations were grouped according to lactation month. Because of the low number of observations in late lactation, records in month 9 and 10 were combined. The number of observations for each size trait within a group ranged from 579 to 1227.

For the same group of heifers, milk production data included 305-day yields on 6618 heifers and 54,475 test-day (TD) yields for milk, fat and protein on 6631 heifers. The number of TD records in the 9 groups ranged from 5743 to 6244.

Multi-trait analyses

The models for size traits included the fixed effects of age at calving, month of calving, pregnancy stage, genetic group, parity of the dam and herd (Koenen and Groen, 1998). The four genetic groups were based on percentage of Holstein-Friesian genes (≤62.5, 75, 87.5 and 100%). Observations on 305-day yield and TD yield for milk, fat and protein for animal *n* were described by the following models:

$$y_{ijkn} = a \times \mathrm{age}_n + \mathrm{hf}_i + \mathrm{h}_j + \mathrm{ys}_k + \mathrm{ani}_n + e_{ijkn}$$
$$\mathrm{td}_{ijlmn} = a \times \mathrm{age}_n + \mathrm{hf}_i + \mathrm{h}_j + \mathrm{la}_l + \mathrm{mo}_m + \mathrm{ani}_n + e_{ijlmn}$$

where

y_{ijkn} = 305-day lactation yield for milk, fat or protein (kg),
td_{ijlmn} = TD yield (kg or g),
a = regression coefficient,
age_n = age at calving (days),
hf_i = fixed effect of genetic group (4 levels),
h_j = fixed effect of herd (560 levels),
ys_k = fixed effect of season of calving (17 levels),
ani_n = random effect of animal,
la_l = fixed effect of lactation stage (21 levels),
mo_m = fixed effect of year × month of observation (26 levels), and
e_{ijklmn} = random error.

Covariances were estimated by DFREML (Meyer, 1991) using an additive genetic relationship matrix including parents and grandparents of the heifers. Analyses started with univariate analyses including all observations across lactation months, i.e. considering observations in all months as observations on the same trait. After that, univariate analyses were performed for the traits within lactation months, followed by bivariate analyses, estimating the covariances between observations in different months. For each trait, the estimated additive genetic covariance matrix (**G**) was then based on the results of the bivariate analyses. To reveal the main sources of variation for a trait, eigenvalues and eigenvectors of **G** were obtained by singular value decomposition.
Genetic correlations between size traits and milk production traits were estimated in bivariate analyses including data across and within monthly groups.

Covariance functions
For each trait, elements of **G** were modelled as a continuous function of lactation stage. The genetic covariance between observations at x_l and x_m months in lactation (standardised to a –1 to 1 scale) was described by the following CF (Kirkpatrick *et al.*, 1990):

$$\mathrm{Cov}(x_l, x_m) = \sum_{i=0}^{p-1} \sum_{j=0}^{p-1} \phi_i(x_l)\, \phi_j(x_m)\, \mathrm{k}_{ij}$$

where
ϕ_i = the ith Legendre polynomial for a pth order of fit,
x = standardised lactation month ($-1 \le x \le 1$), and
k_{ij} = elements of matrix **K**.

In matrix notation **G** was modelled as:

$$\mathbf{G} = \mathbf{\Phi} \mathbf{K} \mathbf{\Phi}' + \mathbf{e}$$

where
G = 9 × 9 variance-covariance matrix from multi-trait analysis,
Φ = 9 × p matrix with orthogonal polynomials,
K = $p \times p$ matrix, and
e = 9 × 9 matrix of random residuals.

Elements of matrix **K** were estimated using generalised least-squares methods, considering elements of **G** as dependent variables (**Y**) and the polynomial values as independent variables (**X**) (Kirkpatrick *et al.*, 1990). The vector including the k_{ij} elements was estimated as $\mathbf{k} = (\mathbf{X'V^{-1}X})^{-1}\mathbf{X'V^{-1}Y}$. Matrix **V** included the sampling errors on the elements of **Y** and was approximated by re-estimating **G** using simulated phenotypic observations based on the estimated genetic and error covariances from the first REML estimates over 50 replicates.

A 9th order Legendre polynomial was the highest order of fit that can be fitted to **G** (full fit) which gives equivalent estimates as a 9 × 9 multi-trait analysis. After analysing a full fit for the additive genetic variance, the order of the polynomial function was decreased sequentially. To test if estimates from a lower order fit were consistent with the REML estimates for **G**, deviations of the lower fit **G** matrix from the full order were tested with a χ^2-distribution (Kirkpatrick *et al.*, 1990). Significant deviations indicate that a model including a lower order polynomial is inconsistent with multi-trait **G**. Furthermore, deviations from estimates for **G** by CF and multi-trait analysis were compared.

RESULTS AND DISCUSSION

Multi-trait analyses

Descriptive statistics and estimated genetic parameters of size traits are in Table 1. Heritability estimates were moderate and varied greatly between different lactation months. However, sampling errors on the monthly estimates were high, e.g. sampling errors for the heritabilities on the monthly data for body weight ranged from 0.11 to 0.18. Mean genetic correlations between observations in different months were all ≥0.92.

Heritabilities for 305-day yields for milk, fat and protein were 0.47, 0.38 and 0.37, respectively (Table 2). Heritabilities for TD records were lowest in the first two months and were generally highest in mid lactation. Mean genetic correlation between observations in different months were 0.89.

Table 1. Phenotypic mean, s.d., heritability (h^2) of full data, range of heritabilities within lactation months and mean genetic correlation (r_g) between observations in different lactation months for body weight, heart girth, hip height, body depth and rump width (n = 7192).

Trait	Mean	±	s.d.	h^2	(range)	r_g	(range)
Body weight	545	±	56 kg	0.47	(0.32 – 0.58)	0.92	(0.71 – 1.00)
Heart girth	192.8	±	7.26 cm	0.40	(0.26 – 0.71)	0.96	(0.78 – 1.00)
Hip height	141.7	±	3.72 cm	0.56	(0.18 – 0.70)	0.99	(0.87 – 1.00)
Body depth[1]	5.22	±	1.57	0.45	(0.23 – 0.69)	0.95	(0.74 – 1.00)
Rump width[1]	4.88	±	1.50	0.34	(0.00 – 0.50)	0.94	(0.59 – 1.00)

[1] Scale: body depth (1 = shallow to 9 = deep) and rump width (1 = narrow to 9 = wide).

Table 2. Phenotypic mean, s.d., heritability (h^2) of full data, range of heritabilities within months of 305-day yield (n = 6618) and test-day yield (n = 54,475) of milk, fat and protein.

	Mean	±	s.d.	h^2 (range)	r_g (range)
305-day yield					
Milk	7113	±	1189 kg	0.47	
Fat	312	±	48 kg	0.38	
Protein	247	±	39 kg	0.37	
Test-day yield					
Milk	23.6	±	5.2 kg	0.33 (0.17 – 0.41)	0.89 (0.49 – 1.00)
Fat	1033	±	209 g	0.22 (0.15 – 0.29)	0.89 (0.44 – 1.00)
Protein	821	±	160 g	0.21 (0.13 – 0.26)	0.89 (0.51 – 1.00)

Table 3. Estimated genetic correlations between body weight, body measurements, conformation traits and 305-day milk, fat and protein yield.

	Milk	Fat	Protein
Body weight	0.13[1]	–0.01	0.11
Heart girth	0.04	–0.14	0.00
Hip height	0.20	0.20	0.18
Body depth	0.26	0.26	0.23
Rump width	0.15	0.23	0.13

[1] Estimated s.e. of the genetic correlations ranged from 0.10 to 0.12.

Based on eigenvalues, the first eigenvector explained a large part of the total variation: the proportion explained by the first eigenvector ranged from 0.89 for rump width to 0.97 for hip height. For milk, fat and protein yield these proportions were 0.91, 0.90 and 0.92, respectively (results not shown). For all traits, elements of the eigenvector associated with the largest eigenvalue had equal signs in all lactation months, indicating that breeding values for size traits in all lactation months were highly correlated. The estimated relative effect of the largest eigenvector agrees with earlier estimates for body weight (Koenen and Veerkamp, 1998) and production (Kirkpatrick *et al.*, 1994; Van der Werf *et al.*, 1998) and indicates that there is a limited amount of trade-off between early and late lactation.

Genetic correlations between size and 305-day yields (Table 3) were moderate for body depth and hip height (0.18 to 0.26) and around zero for body weight and heart girth (–0.14 to 0.13). Genetic correlations between different traits in separate months were highly variable, e.g. the genetic correlation between body weight and milk yield in different months varied from –0.10 to 0.45 (Figure 1).

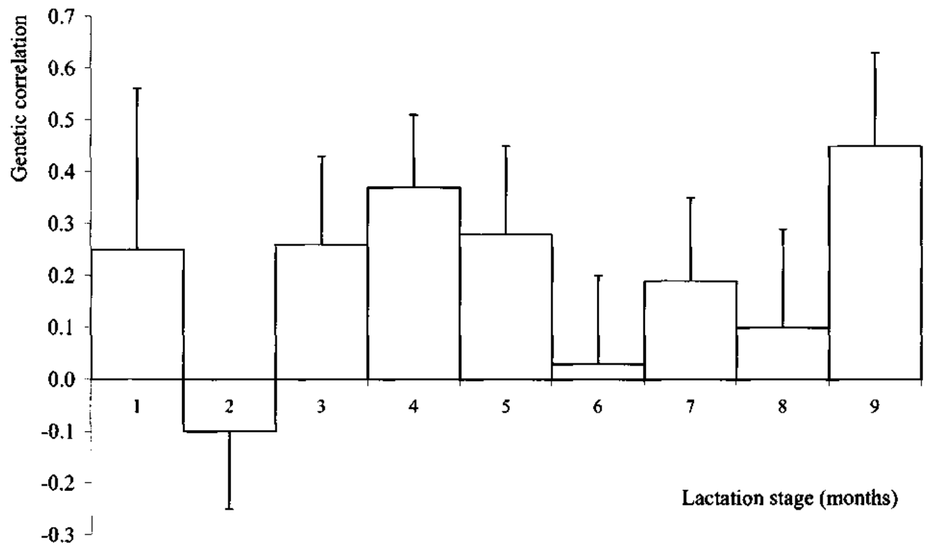

Figure 1. Estimated genetic correlation (± s.e.) between body weight and milk yield during first lactation.

Covariance functions

The order of fit for the lowest order polynomial that did not differ significantly from the full fit was 3 or 5 (Table 4). This means that the number of parameters that is needed to describe the genetic variance was 6 or 15, which is considerable lower that the initial number of 45 that was needed for the multiple trait analyses. To illustrate the effect of smoothing, estimated covariances for heart girth are in Figure 2. The proportion of variance that was explained by the fitted CF ranged from 0.55 for body weight to 0.87 for heart girth. However, it should be noted that covariance matrices derived from some CFs were not positive definite as they had some negative eigenvalues that were close to zero.

Table 4. Order of fit and proportion of explained variance (R^2) of estimated covariance functions for body weight, heart girth, hip height, rump width and body depth.

	Order	R^2
Body weight	5	0.55
Heart girth	3	0.87
Hip height	5	0.75
Rump width	3	0.86
Body depth	3	0.75

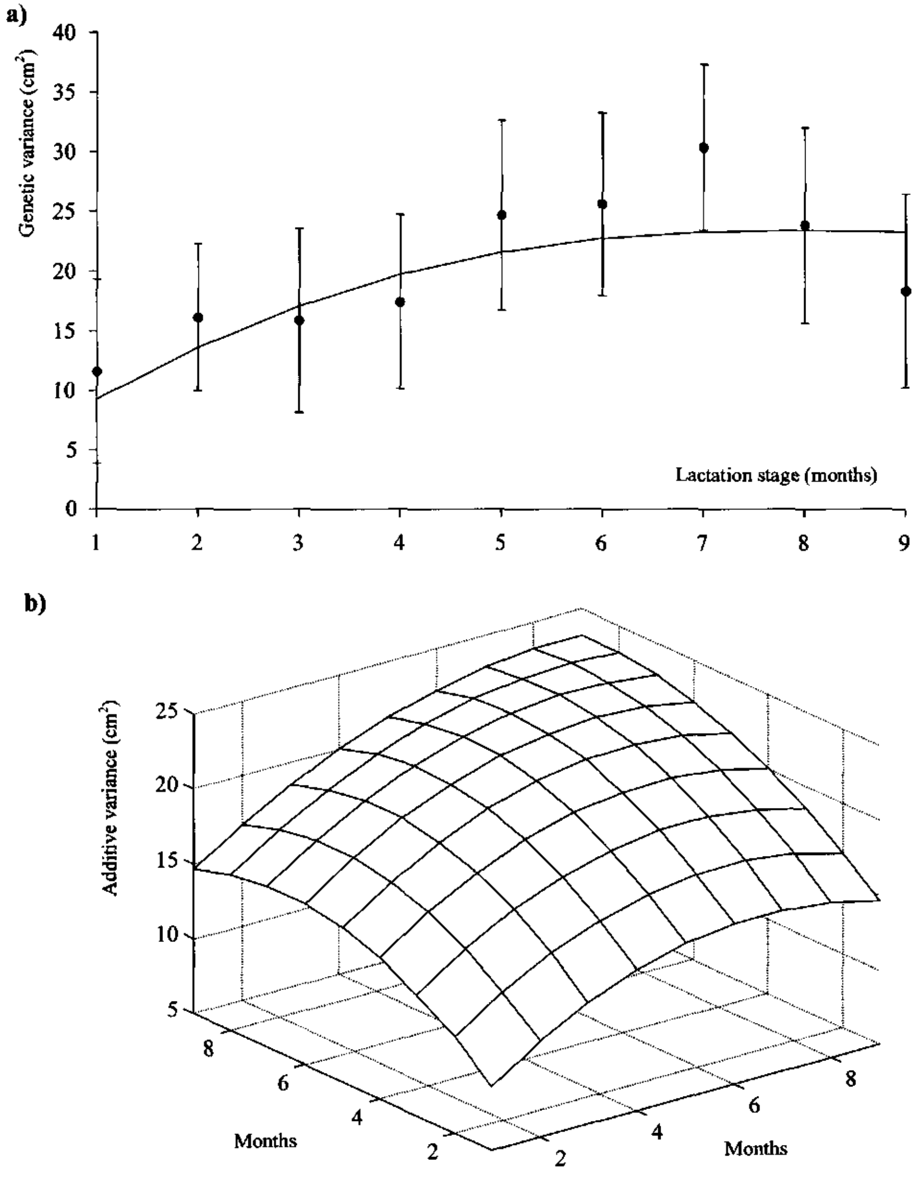

Figure 2. Comparison of REML estimates (± s.e.) and their corresponding estimates from a third order polynomial covariance function (a, smoothed line) and the estimated additive genetic covariance between observations for heart girth during lactation (b).

In this study CF coefficients were estimated by generalised least-squares methods (Kirkpatrick *et al.*, 1990). More recently, also other methods for a continuous description of the variance were suggested. Meyer and Hill (1997) replaced **G** by $\mathbf{\Phi K \Phi'}$ in the multiple-trait mixed model equations and used REML procedures to optimise the likelihood. A further improvement of this method is a direct estimation of **K** from the data using random regression (Meyer, 1998). Although the last method is theoretically most appealing, estimates from random regression using Legendre polynomials can deviate quite largely from covariance estimates based on uni- or bivariate analyses (Van der Werf *et al.*, 1998). When random regression was applied in the present study, large problems with convergence occurred, especially with higher order polynomials. These problems might due to the fact that for size traits no repeated observations on the same animal were available and that all parameters describing the genetic variation had to be estimated via the relationship matrix.

CONCLUSION

Size traits of lactating heifers have a considerable genetic variation. The genetic variation of observations not constant during lactation, but observations are genetically highly correlated (>0.90). Genetic correlations between size traits and 305-day yields for milk, fat and protein are low (–0.14 to 0.26). This study did not indicate significant changes of the correlation between size and yield traits during lactation.

REFERENCES

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Agricultural Research Council, 1980. *The nutrient requirements of ruminant livestock.* Commonwealth Agricultural Bureaux. Slough, England. 351 pp.

Brotherstone, S., 1994. Genetic and phenotypic correlations between linear type traits and production traits in Holstein-Friesian dairy cattle. *Anim. Prod.* 59: 183-187.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research Bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 92-98.

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

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

Koenen, E.P.C. and A.F. Groen, 1998. Genetic evaluation of body weight of lactating Holstein heifers using body measurements and conformation traits. *J. Dairy Sci.* 81: 1709-1713.

Koenen, E.P.C. and R.F. Veerkamp, 1997. *Genotype by diet interactions for live-weight and condition score during lactation in heifers.* Page 38 *in*: Proc. Br. Soc. Anim. Sci. Scarbourough, England.

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. *Livest. Prod. Sci.* 75: 67-77.

Lee, A.J., Boichard, D.A., McAllister, A.J., Lin, Y.C., Nadarajah, T.R., Roy, G.L. and J.A. Vesely, 1992. Genetics of growth, feed intake and milk yield in Holstein cattle. *J. Dairy Sci.* 75: 3145-3154.

Maltz, E., Kroll, O., Spahr, S.L., Devir, S., Genizi, A. and R. Sagi, 1991. Milk yield, parity and cow potential as variables for computerized concentrate supplementation strategy. *J. Dairy Sci.* 74: 2277-2289.

Meyer, K., 1991. *DFREML- a set of programs to estimate variance components by restricted maximum likelihood using a derivative-free algorithm.* User notes version 2.0. University New England. Armidale, Australia. 83 pp.

Meyer, K., 1998. Estimating covariance functions for longitudinal data using a random regression model. *Proc. 6th World Congr. Genet. Appl. Livest. Prod.* 25: 517-520.

Meyer, K. and W.G. Hill, 1997. Estimation of genetic and phenotypic (co)variance functions for longitudinal or "repeated" records by restricted maximum likelihood. *Livest. Prod. Sci.* 47: 185-200.

Misztal, I., Lawlor, T.J., Short, T.H. and P.M. VanRaden, 1992. Multiple-trait estimation of variance components of yield and type traits using an animal model. *J. Dairy Sci.* 75: 544-551.

Schaeffer, L.R. and J.C.M. Dekkers, 1994. Random regressions in animal models for test-day production in dairy cattle. *Proc. 5th World Congr. Genet. Appl. Livest. Prod.* 18: 443-446.

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

Van Elzakker, P.J.M. and J.A.M. Van Arendonk, 1993. Feed intake, body weight and milk production: genetic analysis of different measurements in lactating dairy heifers. *Livest. Prod. Sci.* 37: 37-51.

CHAPTER 7

Genetic analysis of body condition score of lactating Dutch Holstein and Red-and-White heifers

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ABSTRACT

The aim of this study was to estimate phenotypic and genetic parameters for body condition scores (BCS) from the Dutch conformation recording system. Data included 108,809 Dutch Black-and-White (DBW) and 26,208 Dutch Red-and-White (DRW) heifers from 9701 herds that were scored once during lactation on a 1 to 9 scale (1 = emaciated and 9 = obese). Mean BCS for DBW and DRW data was 4.50 and 4.94, respectively. The BCS decreased as percentage of Holstein-Friesian genes increased. For both breeds, BCS after calving was about 5.6 and BCS was lowest at about week 11. For DBW heifers, mean BCS at drying-off was about 0.8 lower than BCS at calving, whereas for DRW heifers BCS was at about the same level as at calving. Variance components were estimated using an animal model including the effects of herd × visit, classifier, age at calving, days in milk and genetic group. The random herd × visit effect explained about 10 to 15% of the phenotypic variation. Heritabilities ranged from 0.24 to 0.38, depending on breed and lactation period. Genetic correlations between BCS observations in bimonthly lactation periods were close to unity, especially for DBW. It was concluded that BCS data collected by conformation classifiers can well be used for genetic evaluation and that genetic variation between animals for BCS-change patterns is a small component of the overall variation in BCS.

INTRODUCTION

Energy balance (EB) in dairy cattle can be defined as the difference between energy intake and energy requirements for milk yield and maintenance. The EB is mostly negative in early lactation (e.g. Berglund and Danell, 1987), which can result in a considerable mobilisation of body adipose (Tamminga *et al.*, 1997). Even though a negative EB is considered to be physiologically normal, size and duration of the negative EB are unfavourably related to health and fertility (Villa-Godoy *et al.*, 1988; Butler and Smith, 1989; Gearhart *et al.*, 1990; Senatore *et al.*, 1996; Domecq *et al.*, 1997b). Although no direct selection on EB is performed, size and duration of EB are affected indirectly by selection for milk yield. With selection for milk yield only, the correlated increase in feed intake is not large enough to cover the increased energy requirements (Gravert, 1985; Van Arendonk *et al.*, 1991). This implies that selection on yield alone is expected to increase the mobilisation of body reserves in early lactation. This is supported by clear evidence form genetic correlations between yield and traits that indicate EB (Veerkamp, 1998) and by studies on high and low genetic merit groups (Buckley *et al.*, 2000). This unfavourable effect of selection on yield might be reduced when information on EB is considered when selection decisions are made (Veerkamp and Koenen, 1999).

Direct information on EB is mostly not available because of missing data on feed intake. However, body condition scores (BCS) are already widely used as an indicator of the amount of stored energy reserves of a dairy cow (Wildman *et al.*, 1982; Edmonson *et al.*, 1989; Broster and Broster, 1998). Until now, BCS data are mostly used for management purposes. These data can also be used for a genetic evaluation when a considerable genetic variation for BCS exists. The resulting estimated breeding values can then be used to improve EB by genetic selection. Knowledge on large-scale data collection and on genetic evaluation for BCS is scarce (Gallo *et al.*, 1999; Jones *et al.*, 1999). In 1998, BCS was introduced in the Dutch conformation scoring system. Therefore, the objective of this study was to estimate phenotypic and genetic parameters for BCS from the two main Dutch dairy cattle breeds.

MATERIAL AND METHODS

Data

Twenty experienced conformation classifiers of NRS collected BCS data for 156,755 lactating heifers from October 1998 through August 1999. These data were collected nationwide as part of the regular conformation classification scheme and included only animals with official herdbook registration. In scoring BCS, classifiers give most attention to the fatty tissue layer at the end of the spinous and transverse processes (loin area), the hip and the pinbones and the tailhead area, based on the system of Lowman *et al.* (1976). For practical reasons, two modifications were used. First, classifiers scored on a 1 to 9 scale (1 = emaciated, 5 = average and 9 = obese) with increments of 1, rather than on the more commonly used 1 to 5 scale with increments of a quarter or half. The reason for this modification was that other linear conformation traits were already scored on the 1 to 9 scale. Secondly, only a visual assessment of the energy reserves was performed without palpating the cows to assess the amount of tissue under the skin.

The total data file was split into two files according to breed: either Dutch Black-and-White (DBW) or Dutch Red-and-White (DRW). Heifers in the DBW and DRW data mainly originate from the Dutch-Friesian and Maas-Rijn-IJssel population, respectively, but have been upgraded with Holstein-Friesian genes. In this study, the DBW and DRW population included 94 and 67% of Holstein-Friesian genes, respectively.

Classifiers with <500 observations were removed from the data. Although classifiers were instructed to assume a s.d. for BCS of 1.5, s.d. within classifiers ranged from 1.1 to 1.8. To account for this heterogeneity, phenotypic observations were standardised to a s.d. of 1.5 within classifiers. Furthermore, calving age had to be between 20 and 35 months. Repeated observations on the same heifer, observations from herds with less than five records and records on heifers scored after 305 days in milk or from an unknown sire were removed. Finally, the DBW data file included 108,809 heifers from 7524 herds and the DRW data file included 26,208 heifers from 2177 herds. Heifers in the DBW and DRW data were of 3632 and 963 sires, respectively; maximum number of daughters per sire was 9063 and 3370 for DBW and DRW, respectively.

Statistical model

First, all observations on BCS were considered as observations on the same trait, i.e. it was assumed that genetic variance is constant during lactation and that genetic correlations between BCS in different lactation periods are unity.

Preliminary analyses using PROC GLM (SAS®, 1990) were used to evaluate the regression of age at calving and days in milk on BCS. For the regression on days in milk, orthogonal Legendre polynomials (Ambramowitz and Stegun, 1965) were used to reduce problems with high order polynomials. As Legendre polynomials are only defined for variables in the range −1 to 1, days in milk (1 to 305) were standardised to this range. The effects of age at calving and days in milk were adequately described by a second and fifth order polynomial, respectively. Order of these polynomials was established by including parameters that differed significantly ($P < 0.01$) from zero. In the DBW data, a sixth-order polynomial on days in milk was still significant but explained little variation. Therefore, a fifth-order polynomial was used for both breeds.

Fixed effects and variance components were estimated with an animal model including pedigree of the scored heifers that was traced for two generations. Parents with only one offspring in the data were treated as unknown parents to reduce computational efforts. The additive genetic relation matrix included 217,589 and 51,673 animals for DBW and DRW, respectively. Unknown parents in the pedigree were assigned to four genetic groups (Westell *et al.*, 1988). These groups were defined according to the main breed composition (>50% Holstein-Friesian, >50% Dutch-Friesian, >50% Maas-Rijn-IJssel and other breeds). The final model for BCS data is represented by:

$$\mathrm{BCS}_{ijk} = a_1 \times \mathrm{age} + a_2 \times \mathrm{age}^2 + \sum_{n=1}^{5} \beta_n t^n + \mathrm{class}_i + \mathrm{hv}_j + \mathrm{ani}_k + e_{ijk}. \quad (1)$$

where

BCS_{ijk} = BCS,

a_1, a_2 = regression coefficients,

age = age at first calving,

β_n, = regression coefficients for the Legendre polynomials,

t = standardised days in milk,

class_i = fixed effect of classifier (20 levels),

hv_j = random effect of herd × visit (8529 and 2584 for DBW and DRW, respectively),

ani_k = random effect of animal, and

e_{ijk} = random residual.

Estimates for the fixed effects and variance components were obtained using restricted maximum likelihood methods (Gilmour *et al.*, 1999).

Secondly, the assumption of the same genetic background across lactation periods is tested by estimating genetic parameters within five bimonthly lactation periods (month 1-2, month 3-4, month 5-6, month 7-8 and month 9-10), followed by the estimation of genetic correlations between periods using model (1). As a complete multivariate analysis (five traits) gave large computational problems, genetic correlations were estimated in bivariate analyses. Within a bivariate analysis, estimates for the fixed effects were assumed to be the same for both traits.

RESULTS

Phenotypic means

Unadjusted phenotypic mean for DBW and DRW heifers were 4.50 ± 1.55 and 4.94 ± 1.51, respectively. The difference between breeds is illustrated by BCS means for breed groups with ≥500 heifers. In the DBW data, BCS decreased as percentage of Holstein-Friesian genes increased (Figure 1). In the DRW data, BCS increased as percentage of Maas-Rijn-IJssel genes increased (Figure 2).

The regression on age at calving showed for both breeds that BCS increased as calving age increased: mean BCS of heifers calving at the maximum age (35 months) was about 0.6 higher than of heifers calving at the minimum age (20 months).

The effect of days in milk on BCS is illustrated in Figure 3 by unadjusted weekly means for BCS and the fitted polynomial regressions from model 1. The unadjusted means were based on 26 to 3486 scored heifers per lactation week; especially in the first and last lactation weeks numbers of observations were small. Average BCS at calving was about 5.6 for both breeds. Decrease in BCS was largest during the first lactation weeks. Days in milk with minimum BCS and the magnitude of BCS-loss were derived from the fitted polynomial regression. For both breeds, BCS was at minimum at week 11. Average BCS-loss was greater for DBW (1.2) than for DRW (1.0). After reaching minimum BCS, BCS increased gradually until the end of lactation. At the end of the 305-day lactation period, mean BCS of DBW heifers was substantially lower than BCS at calving, whereas mean BCS of DRW heifers was at about the same level as at calving.

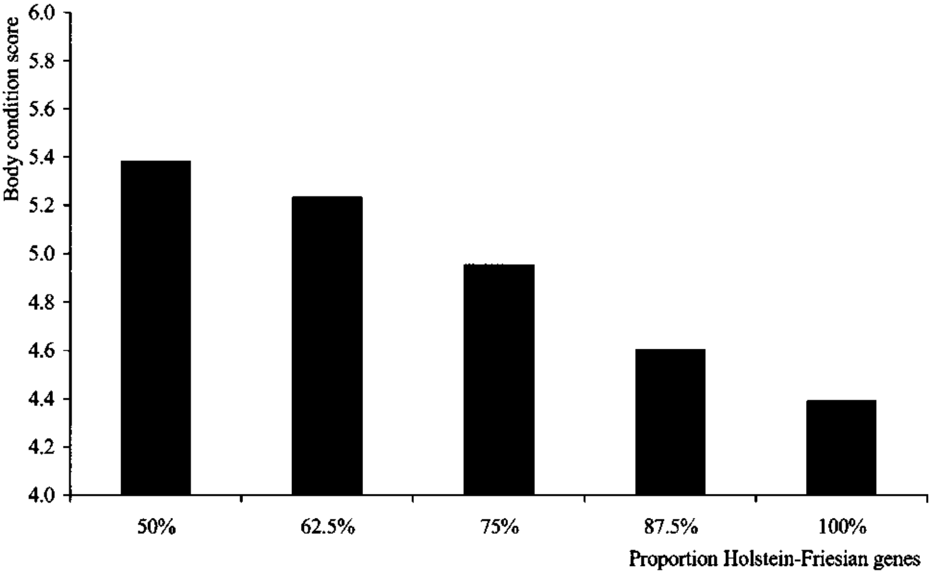

Figure 1. Mean body condition score for Black-and-White heifers by proportion of Holstein-Friesian genes.

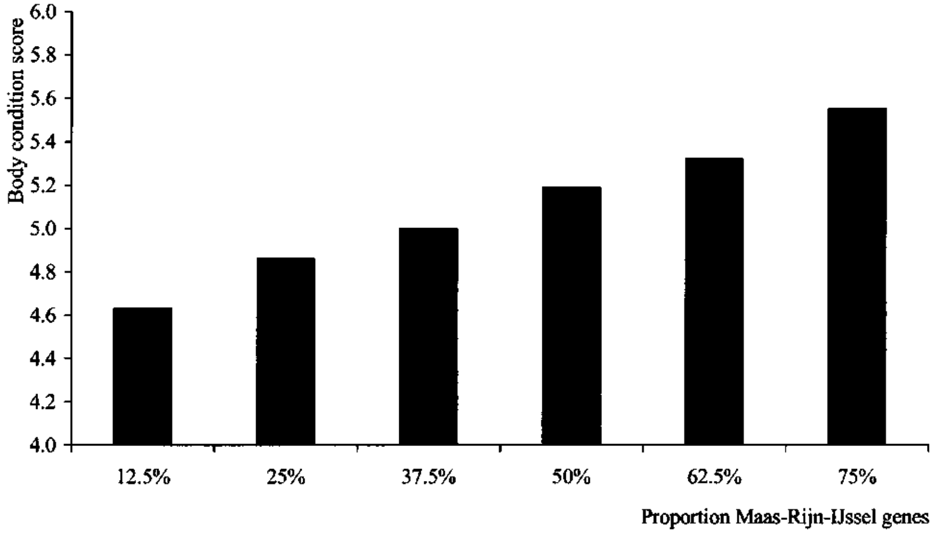

Figure 2. Mean body condition score for Red-and-White heifers by proportion of Maas-Rijn-IJssel genes.

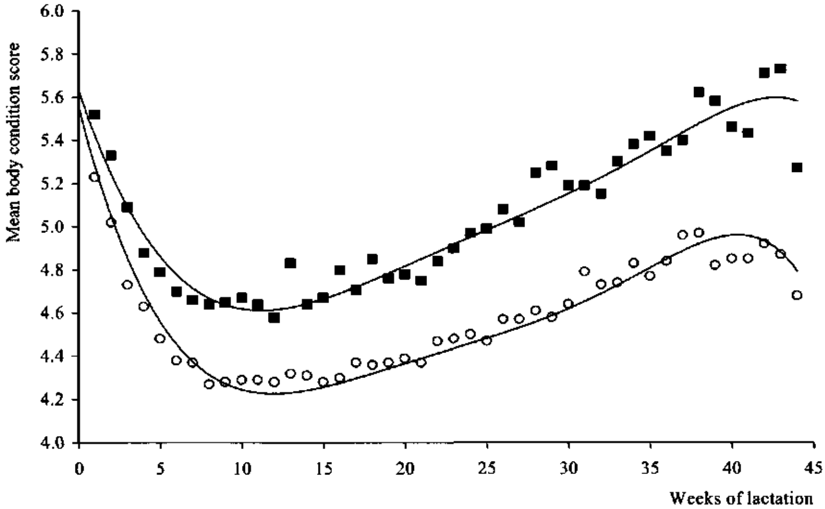

Figure 3. Unadjusted means and fitted polynomial regression on days in milk for body condition score of Black-and-White (○) and Red-and-White (■) heifers during first 44 weeks of lactation

Variance components

Estimated variance components and heritabilities for BCS across lactation periods are in Table 1. Between-herd variance accounted for about 10 to 15% of the total variance in all models. Heritability was higher for DBW (0.38) than for DRW (0.30). Unadjusted means and estimates for the variance components and heritabilities for BCS within bimonthly lactation periods are in Table 2. Unadjusted s.d. for BCS tended to increase slightly with later lactation periods. Heritability estimates within lactation periods ranged from 0.23 to 0.37. Heritability was lowest in the first period and highest in the second period. Estimates for the genetic correlations between BCS observations in different lactation periods are in Table 3. Genetic correlations between BCS in different lactation periods were close to unity, especially in the DBW data. In the DRW data, genetic correlations tended to decrease slightly as time period between observations increased. The high genetic correlations indicated that the genetic variation in BCS-changes during lactation is limited.

Table 1. Number of observations, mean, s.d. and estimates for herd × visit variance (σ^2_{hv}), genetic variance (σ^2_a), residual variance (σ^2_e) and heritability (h^2) for body condition score in Black-and-White and Red-and-White heifers.

Data file	n	Mean ± s.d.	σ^2_{hv}	σ^2_a	σ^2_e	h^2
Black-and-White	108,809	4.50 ± 1.55	0.241	0.864	1.160	0.38 ± 0.02
Red-and-White	26,208	4.94 ± 1.51	0.287	0.665	1.235	0.30 ± 0.03

Table 2. Number of observations, mean ± s.d., herd × visit variance (σ^2_{hv}), genetic variance (σ^2_a), error variance (σ^2_e) and heritability for body condition score in different lactation periods in Black-and-White and Red-and-White heifers.

	Black-and-White						Red-and-White					
Month	n	Mean ± s.d.	σ^2_{hv}	σ^2_a	σ^2_e	h^2	n	Mean ± s.d.	σ^2_{hv}	σ^2_a	σ^2_e	h^2
1 – 2	18,209	4.48 ± 1.54	0.300	0.601	1.226	0.28[1]	4418	4.80 ± 1.45	0.333	0.455	1.186	0.23
3 – 4	29,348	4.31 ± 1.50	0.229	0.827	1.159	0.37	6968	4.69 ± 1.46	0.230	0.657	1.192	0.32
5 – 6	26,941	4.43 ± 1.52	0.284	0.725	1.253	0.32	6467	4.86 ± 1.50	0.343	0.528	1.312	0.24
7 – 8	22,826	4.68 ± 1.56	0.312	0.755	1.287	0.32	5774	5.22 ± 1.52	0.363	0.603	1.284	0.27
9 – 10	11,485	4.87 ± 1.61	0.420	0.729	1.342	0.29	2581	5.48 ± 1.54	0.370	0.626	1.316	0.27

[1] Standard errors of the heritabilities ranged from 0.03 to 0.05 for Black-and-White and from 0.05 tot 0.07 for Red-and-White.

Table 3. Genetic correlations between body condition scores in different lactation periods for Black-and-White and Red-and-White heifers.

	Black-and-White					Red-and-White				
Month	1 – 2	3 – 4	5 – 6	7 – 8	9 – 10	1 – 2	3 – 4	5 – 6	7– 8	9 – 10
1 – 2	-	0.99	0.99	0.97	0.99	-	0.98	0.94	0.90	0.87
3 – 4		-	1.00	1.00	1.00		-	1.00	0.93	0.88
5 – 6			-	0.99	0.97			-	0.89	0.86
7 – 8				-	1.00				-	1.00
9 – 10					-					-

DISCUSSION

The aim of this study was to estimate phenotypic and genetic parameters for BCS data from a field-recording scheme. As heifers can be scored at all moments in lactation, adequate adjustments for days in milk are needed when field data are used for a genetic evaluation. The estimated loss in BCS in this study is in line with results of Ruegg and Milton (1995) and Domecq *et al.* (1997b). However, several earlier studies reported lower estimates. For UK Holstein heifers, Jones *et al.* (1999) found an average BCS loss of only 0.4. On a five-point scale, both Waltner *et al.* (1993) and Gallo *et al.* (1996) reported a BCS loss of about 0.3, whereas Ruegg and Milton (1995) estimated a BCS loss of 0.7. The higher estimate for BCS loss in this study might be related to the use of a fifth-order polynomial to model the effect of days in milk, whereas Gallo *et al.* (1996) and Jones *et al.* (1999) used cubic polynomials. When cubic polynomials were fitted to our data, predicted BCS agreed well with observed BCS in mid and late lactation but not in early lactation. Evaluation of the residuals showed that BCS in early lactation was systematically underestimated, which resulted in an underestimated BCS loss.

The higher BCS loss of DBW (1.2) compared to DRW (1.0) might be related to the higher production level of DBW. On the national level, average milk yield of DBW cows was about 1000 kg higher than of DRW cows (8003 *vs.* 6975 kg; NRS, 1999). Positive relations between BCS loss and production level have been reported (Waltner *et al.*, 1993; Ruegg and Milton, 1995; Gallo *et al.* 1996; Domecq *et al.*, 1997a).

The moment with minimum BCS was about week 11 in our study, which was later than literature estimates for the moments of maximum milk yield and minimum BW (Wood *et al.*, 1980; Gravert, 1985; Berglund and Danell, 1987) which might suggest that changes in BCS do not fully reflect changes in EB.

This study found considerable heritabilities for BCS data from the Dutch conformation classification scheme based on only visual assessment of BCS. These heritabilities were slightly higher than literature estimates for field data.

Heritability estimates for Holstein heifers from the UK ranged from 0.20 to 0.28 (Jones *et al.*, 1999). For Italian-Friesian cows, a heritability of 0.29 was reported (Gallo *et al.*, 1999).

The high genetic correlations between BCS observations from different lactation periods agree with earlier estimates. Koenen and Veerkamp (1998) found very high genetic correlations (0.84-1.00) between BCS observations of heifers during the first 26 weeks of lactation. Dechow *et al.* (1999) found genetic correlations >0.90 for BCS data from different lactation moments. Estimates from Jones *et al.* (1999) were somewhat lower: genetic correlations among BCS observations in different months ranged from 0.63 to 1.00 (on average 0.89). Gallo *et al.* (1999) found genetic correlations between lactation periods in the range from 0.70 to 0.97. The small changes in genetic variances across lactation periods and the high genetic correlations imply that BCS scores from various lactation periods are genetically similar and that genetic variation among animals for BCS changes during lactation is limited. In practice, this means that BCS observations from all lactation periods can be used in a similar way when the aim is to estimate breeding values for mean BCS during first lactation.

This study showed that breeding values for BCS can easily be obtained from the regular conformation recording system. For example, in the Dutch situation about 60 daughters are scored when the first breeding value for milk yield becomes available, the accuracy of an estimated breeding value would be about 0.92. Although BCS has no explicit economic value, it might provide additional genetic information on traits that relate to EB such as milk production, feed intake, health and fertility. The optimal use of a breeding value for BCS in combination with breeding values for other traits therefore largely depends on the genetic relationships with these traits. For example, Pryce *et al.* (2000) found a clear genetic correlation between BCS and calving interval and suggested the use of BCS as a tool to improve fertility. However, as knowledge on most of these relationships is still scarce, further studies are needed before the optimal breeding strategy including genetic information on BCS can be established.

REFERENCES

Ambramowitz, M. and I.A. Stegun, 1965. *Handbook of mathematical functions with formulas, graphs and mathematical tables.* Dover publications Inc. New York, USA. 1045 pp.

Berglund, B. and B. Danell, 1987. Live weight changes, feed consumption, milk yield and energy balance in dairy cattle during the first period of lactation. *Acta Agr. Scand.* 37: 495-509.

Broster, W.H. and V.J. Broster, 1998. Body score of dairy cows: review. *J. Dairy Res.* 65: 155-173.

Buckley, F., Dillon, P., Crosse, S., Flynn, F. and M. Rath, 2000. The performance of Holstein Friesian dairy cows of high and medium genetic merit for milk production on grass-based feeding systems. *Livest. Prod. Sci.* 64: 107-119.

Butler, W.R. and R.D. Smith, 1989. Interrelationships between energy balance and postpartum reproductive function in dairy cattle. *J. Dairy Sci.* 72: 767-783.

Dechow, C.D., Rogers, G.W. and J.S. Clay, 1999. Heritabilities, genetic correlations and phenotypic correlations for producer-recorded body condition scores within lactations. *J. Dairy Sci.* 82 (Suppl. 1): 116.

Domecq, J.J., Skidmore, A.L., Lloyd, J.W. and J.B. Kaneene, 1997a. Relationship between body condition scores and milk yield in a large dairy herd of high yielding Holstein cows. *J. Dairy Sci.* 80: 101-112.

Domecq, J.J., Skidmore, A.L., Lloyd, J.W. and J.B. Kaneene, 1997b. Relationship between body condition scores and conception at first artificial insemination in a large dairy herd of high yielding Holstein cows. *J. Dairy Sci.* 80: 113-120.

Edmonson, A.J., Lean, I.J., Weaver, L.D., Farver, T. and G. Webster, 1989. A body condition scoring chart for Holstein dairy cows. *J. Dairy Sci.* 72: 68-78.

Gallo, L., Carnier, P., Cassandro, M., Dal Zotto, R. and G. Bittante, 1999. *Genetic aspects of condition score, heart girth and milk yield traits in Italian Friesian herds.* Pages 159-164 *in* Oldham, J.D., Simm, G., Groen, A.F., Nielsen, B.L., Pryce, J.E. and T.L.J. Lawrence (Eds.). Metabolic stress in dairy cows: proceedings of an international symposium. BSAS. Edinburgh, Scotland.

Gallo, L., Carnier, P., Cassandro, M., Mantovani, R., Bailoni, L., Contiero, B. and G. Bittante, 1996. Change in body condition score of Holstein cows as affected by parity and mature equivalent milk yield. *J. Dairy Sci.* 79: 1009-1015.

Gearhart, M.A., Curtis, C.R., Erb, H.N., Smith, R.D., Sniffen, C.J., Chase, L.E. and M.D. Cooper, 1990. Relationship of changes in condition score to cow health in Holsteins. *J. Dairy Sci*. 73: 3132-3140.

Gilmour, A.R., Cullis, B.R., Welham, S.J. and R. Thompson, 1999. *ASREML user manual.* 164 pp.

Gravert, H.O., 1985. Genetic factors controlling feed efficiency in dairy cows. *Livest. Prod. Sci.* 13: 87-99.

Jones, H.E., White, I.M.S. and S. Brotherstone, 1999. Genetic evaluation of Holstein-Friesian sires for daughter condition-score changes using a random regression model. *Anim. Sci.* 68: 467-475.

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. *Livest. Prod. Sci.* 57: 67-77.

Lowman, B.G., Scott, N.A. and S.H. Somerville, 1976. *Condition scoring of cattle.* Rev. ed. Bull. 6. The East of Scotland College of Agriculture. Edinburgh, Scotland. 31 pp.

NRS, 1999. *Jaarstatistieken NRS.* CR Delta. Arnhem, The Netherlands. 62 pp.

Pryce, J.E., Coffey, M.P. and S. Brotherstone, 2000. The genetic relationship between calving interval, body condition score and linear type and management traits in registered Holsteins. *J. Dairy Sci.* 83: 2664-2671.

Ruegg, P.L. and R.L. Milton, 1995. Body condition scores of Holstein cows on Prince Edward Island, Canada: relationships with yield, reproductive performance and disease. *J. Dairy Sci.* 78: 552-564.

SAS®, 1990. *Language: Reference. Version 6.* 1st ed. SAS Institute. Cary NC, USA. 1042 pp.

Senatore, E.M., Butler, W.R and P.A. Oltenacu, 1996. Relationships between energy balance and post-partum ovarian activity and fertility in first lactation dairy cows. *Anim. Sci.* 62: 17-23.

Tamminga, S., Luteijn, P.A. and R.G.M. Meijer, 1997. Changes in composition and energy content of liveweight loss in dairy cows with time after parturition. *Livest. Prod. Sci.* 52: 31-38.

Van Arendonk, J.A.M., Nieuwhof, G.J., Vos, H. and S. Korver, 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. *Livest. Prod. Sci.* 29: 263-275.

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. and E.P.C. Koenen, 1999. *Genetics of food intake, liveweight, condition score and energy balance.* Pages 63-73 *in* Oldham, J.D., Simm, G., Groen, A.F., Nielsen, B.L., Pryce, J.E. and T.L.J. Lawrence (Eds.). Metabolic stress in dairy cows: proceedings of an international symposium. BSAS. Edinburgh, Scotland.

Villa-Godoy, A., Hughes, T.L., Emery, R.S., Chapin, L.T. and R.L. Fogwell, 1988. Association between energy balance and luteal function in lactating dairy cows. *J. Dairy Sci.* 71: 1063-1072.

Waltner, S.S., McNamara, J.P. and J.K. Hillers, 1993. Relationships of body condition score to production variables in high producing Holstein dairy cattle. *J. Dairy Sci.* 76: 3410-3419.

Westell, R.A., Quaas, L.R. and L.D. Van Vleck, 1988. Genetic groups in an animal model. *J. Dairy Sci.* 71: 1310-1318.

Wildman, E.E., Jones, G.M., Wagener, P.E., Boman, R.L., Troutt Jr., H.F. and T.N. Lesch, 1982. A dairy cow body condition scoring system and its relationship to selected production characteristics. *J. Dairy Sci.* 65: 495-501.

Wood, P.D.P., King J.O.L. and P.G. Youdan, 1980. Relationships between size, liveweight change and milk production characters in early lactation in dairy cattle. *Anim. Prod.* 31: 143-151.

CHAPTER 8

Economic values of live weight and feed-intake capacity of dairy cattle under Dutch production circumstances

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ABSTRACT

This study estimated the effect of genetic change of live weight (LW) and dry-matter intake capacity (DMIC) on labour income (economic values) in dairy cattle under different production circumstances. Dutch production circumstances in the years 1998 and 2008 were based on different scenarios and varied with respect to product prices, milk output restrictions and environmental legislation. Linear programming was used to maximise labour income at farm level. Economic values (EV) for LW ranged from –0.29 to –0.17 €/kg/cow/year and depended on beef prices and marginal feed costs. Economic values for DMIC ranged from 18 to 40 €/kg/cow/year and depended on the difference between marginal costs of roughage and concentrates. Estimated EVs were highly sensitive to levels of DMIC and milk production. At higher DMIC levels, the EV for LW increased, whereas the EV for DMIC decreased. At higher milk production levels, the EV for LW decreased whereas the EV for DMIC increased.

INTRODUCTION

Most dairy cattle breeding schemes do not include live weight (LW) or dry-matter intake capacity (DMIC) in the breeding objective. For LW, large-scale genetic evaluations only exist in New Zealand (Ahlborn and Dempfle, 1992) and Finland (Hietanen and Ojala, 1995).

Including LW and DMIC in the breeding goal can be profitable when genetic variance for LW and DMIC exists and when genetic changes improve the efficiency of the dairy cattle production system. The variation in LW and DMIC has considerable genetic influence: heritability estimates are about 0.45 and 0.35, respectively (Veerkamp, 1998).

The economic value (EV) of a trait expresses the extent that economic efficiency of production is improved by an increase of that trait at the moment of expression. The EV is derived as the marginal revenues after increasing the genetic merit of a trait by one unit, while keeping all other traits in the aggregate genotype constant. Efforts have been made to estimate the EV of LW (e.g. VanRaden, 1988) and DMIC (e.g. Groen and Korver, 1989). The EV of LW is related to feed costs for maintenance requirements and returns from beef production. The EV of DMIC is related to the relative costs of roughages and concentrates. In most situations, DMIC limits roughage intake such that the energy and protein requirements are not completely met and concentrates have to be supplemented. When roughage is the cheapest feed available, genetic improvement of DMIC increases profitability (Köhne, 1968).

Estimates for the EVs depend on the definition of the production system, the goals to be optimised and particular production circumstances (Groen *et al.*, 1997). A production system can be defined at different levels, e.g. animal, farm or sector level (Groen, 1989a). Production systems can be optimised to different goals, e.g. maximum profit, minimal costs of product or maximum return on investment (Harris, 1970). Many studies on dairy cattle breeding maximised labour income (remuneration for labour and management that is left over after all other costs have been paid). Circumstances that limit input or output, e.g. a quota system for milk production or environmental legislation, might effect the EV of a trait (Groen, 1989c). It is not fully clear from literature what the EVs of LW and DMIC will be under expected future production circumstances with different market situations, production intensities and environmental legislation.

The aims of this paper are to review literature estimates for the EV of LW and DMIC and to estimate these EVs for Holstein-Friesian dairy cattle under current and possible future production circumstances.

LITERATURE

Literature estimates for the EV of LW have been derived using different bio-economic models (Table 1). Most studies modelled the effect of genetic changes at animal level. Groen (1989b,c) simulated the effect of genetic improvement using a model that described traits during the life cycle of a dairy cow. Steverink *et al.* (1994a) and Visscher *et al.* (1994) modelled the production system at farm level. The study of Van der Werf *et al.* (1998) modelled beef production at sector level and simultaneously evaluated the effect of increased LW in dairy cows on costs and revenues from veal calves, fattening bulls and culled cows.

Model elements that were considered in estimating EVs varied among studies. Most studies included energy requirements and beef production. VanRaden (1988) also considered higher costs for housing and fertility problems associated with a higher LW. Steverink *et al.* (1994a) defined a model at farm level that also included grass and maize production.

Different restrictions on input or output of the production system have been imposed. Milk output was restricted by the milk quota system for European situations (Groen, 1989c; Steverink *et al.*, 1994a). Feed input at farm level was restricted for pasture-based production systems in New Zealand (Dempfle, 1989) and Australia (Visscher *et al.*, 1994). An example of environmental restrictions is the inclusion of levies for nutrient surpluses above acceptable levels (Steverink *et al.*, 1994a).

Estimated EVs for LW ranged from –1.28 to 0.02 €/kg/cow/year. In most studies, marginal feed costs exceeded marginal beef returns when increasing LW. Estimated EVs for LW were more negative when roughage input was restricted (Dempfle, 1989; Groen, 1989c; Visscher *et al.*, 1994). With a fixed roughage input

Table 1. Model characteristics and estimates for the economic value for live weight.

Source	Level	Elements	Restrictions	Economic value (€/kg/cow/year)[1]
VanRaden, 1988	Animal	Beef production Energy requirements[2] Housing Health and fertility	-	–0.23
Dempfle, 1989	Animal	Beef production Energy requirements	Farm roughage input	–0.11
Groen, 1989b	Animal	Beef production Energy requirements	-	–0.46 to –0.39
Groen, 1989c	Farm	Beef production Energy requirements	Roughage input Milk output	–1.28 to –0.42
Steverink *et al.*, 1994a	Farm	Beef production Energy requirements Protein requirements Crop production	Milk output Nitrogen use Phosphate use	–0.17 to 0.02
Visscher *et al.*, 1994	Farm	Beef production Energy requirements	Roughage input	–0.42 to –0.34
Veerkamp, 1996	Animal	Energy requirements	-	–0.64 to –0.41
Harris, 1998	Farm	Beef production Energy requirements	Dry-matter intake	–0.25 to –0.19
Van der Werf *et al.*, 1998	Sector	Beef production[3] Energy requirements	-	–0.21

[1] 1.00 € = 0.58 AUD = 0.68 GBP = 0.45 NLG = 0.49 NZD = 0.91 USD.

[2] Requirements for growth and maintenance.

[3] Based on a dressing percentage of 50%.

Table 2. Model characteristics and estimates for the economic value for dry-matter intake capacity.

Source	Level	Elements	Restrictions	Economic value (€/(kg/day)/cow/year)[1]
Groen and Korver, 1989	Animal	Energy requirements[2] Feed alternatives	-	2 to 17
Zeddies, 1992	Animal	Energy requirements Feed alternatives	-	77 to 164
Steverink *et al.*, 1994a	Farm	Energy requirements Protein requirements Feed alternatives Crop production	Milk output Nitrogen use Phosphate use	0 to 3
Berentsen and Giessen, 1996	Farm	Energy requirements Protein requirements Feed alternatives Crop production	Milk output Nitrogen surplus Phosphate surplus	7 to 37
Veerkamp, 1996	Animal	Energy requirements Feed alternatives	-	5 to 27

[1] 1.00 € = 0.51 DM = 0.68 GBP = 0.45 NLG.

[2] Requirements for growth and maintenance.

per farm, increased maintenance feed requirements per cow resulted in a reduction of the number of cows and consequently in a lower milk output per farm. Also in situations with restrictions on nutrient surpluses, EVs for LW were more negative as a result of higher marginal feed costs (Steverink *et al.*, 1994a).

Most studies that derived EVs for DMIC (Table 2) defined DMIC as the maximum daily *ad libitum* feed intake in kg dry-matter (DM) of a reference feed (e.g. pasture grass cut at the grazing stage of first growth; Jarrige *et al.*, 1986). Other elements in the models were energy and protein requirements, availability of feeds and their corresponding costs. Most studies included two different feed stuffs (Groen and Korver, 1989; Veerkamp, 1996) or more (Berentsen and Giessen, 1996).

Estimated EVs for DMIC ranged from 0 to 164 €/(kg/day)/cow/year (Table 2). The large variation might be related to assumed milk production levels and marginal feed costs. In the study of Steverink *et al.* (1994a), EVs for DMIC were mostly zero as DMIC was not limiting the formulation of the cheapest diet at a milk production level of 6000 kg. At higher production levels, Berentsen and Giessen (1996) found positive EVs as DMIC became limiting.

The EV of DMIC was highly sensitive to the price difference between roughage and concentrates (Groen and Korver, 1989). Some studies assumed feed costs to be fixed (e.g. Groen and Korver, 1989; Veerkamp, 1996), whereas in other studies (Steverink *et al.*, 1994a; Berentsen and Giessen, 1996) marginal feed costs varied with specific production circumstances.

At lower production intensities (<12,000 kg milk/ha) marginal costs for roughage are generally lower than at a higher production intensity (16,000 kg milk/ha) which results in increased EVs for roughage, whereas an opposite trend can be seen when restrictions on nutrient surpluses are imposed (Steverink *et al.*, 1994a).

MATERIALS AND METHODS

In the present study, EVs for LW and DMIC were estimated at farm level under four different production circumstances. Including average 1998 production circumstances, three scenarios were defined for possible production circumstances in 2008 based on expected technological improvements and planned market and price policy. Linear programming techniques were then used to maximise labour income under all defined production circumstances.

Scenarios

Production circumstances for 1998 (1998-Actual) are based on actual data (Table 3). The first scenario for the situation in 2008 (2008-Trend) includes a moderate market liberalisation within the European Union (EU). The second scenario (2008-Liberal) includes a complete market liberalisation policy; i.e. abolition of milk quotas and price intervention. The third scenario (2008-LTO) is in line with the 2008-Trend scenario but includes two additional environmental restrictions. First, present plans of the Dutch farmers organisation LTO (LTO, 1998) promote a ground-based production system in which input of roughages at farm level is excluded. Secondly, a more severe restriction on stocking density is included in order to comply with the European nitrate directive (European Commission, 1991).

Farm characteristics

In the period 1990/1991 to 1996/1997, farm size of the average Dutch specialised dairy herd increased from 29.1 to 33.0 ha, representing a mean increase in land of about 0.7 ha/year (LEI-DLO, 1998a). Farm size is therefore set to 33 ha for the 1998-Actual scenario and to 40 ha for all scenarios in 2008. In the same period, milk quota of these farms increased from 334,666 to 389,548 kg, representing a mean increase of about 9000 kg/year (LEI-DLO, 1998a). Milk quota in the 1998-Actual scenario is set to 390,000 kg and to 480,000 kg for the 2008-Trend and 2008-LTO scenario. No milk quota is included in the 2008-Liberal scenario.

Table 3. Milk quota, maximum nitrogen and phosphate surpluses, levies on surpluses and maximum stocking densities for 1998 and 2008.

			2008		
		1998-Actual	Trend	Liberal	LTO
Milk quota (kg/year)		390,000	480,000	-	480,000
Maximum surplus (kg/ha)					
Nitrogen	grassland	300	180	180	180
	other	175	100	100	100
Phosphate		40	20	20	20
Levy on exceeded surplus (€/kg)					
Nitrogen		0.68	0.68	0.68	0.68
Phosphate	≤ 5 kg	-	2.27	2.27	2.27
	> 5 kg	-	9.08	9.08	9.08
	≤ 10 kg	1.13	-	-	-
	> 10 kg	4.54	-	-	-
Maximum stocking density (grazing units/ha)		-	2.5	2.5	2.0

Environmental restrictions

From 1998 onwards, Dutch legislation requires monitoring of nitrogen and phosphate input (purchased feed and fertiliser) and output (sold milk, beef and sold manure) at farm level (MNLV, 1997). For both nutrients, there is a ceiling on acceptable surplus (differences between input and output). A levy is applied for each kg per ha of realised surplus exceeding this maximum (MNLV, 1997). Environmental restrictions for the scenarios in 2008 are based on present legislation that defines these maximum levels for years up to 2006 (MNLV, 1997). For production circumstances in 2008, acceptable surpluses are lower and levies on phosphate surpluses are higher than in the 1998-Actual scenario (Table 3). For nitrogen, the levy is 0.68 €/kg in all situations. For phosphate, the levy depends on the amount of surplus. For the 1998 scenario, it is 1.13 €/kg for the first 10 kg of surplus/ha and 4.54 €/kg for surpluses >10 kg. For the 2008 scenarios, the levy is 2.27 €/kg for the first 5 kg of surplus per ha above the ceiling and 9.08 €/kg for surpluses >5 kg.

For 2008, restrictions on stocking density are based on the number of grazing units per hectare. A grazing unit is based on the annual production of phosphate and is set to 1 for a mature dairy cow. A growing heifer and a calf represent 0.43 and 0.22 grazing unit, respectively (MLNV, 1997). Maximum stocking density is 2.5 grazing units per ha in the 2008-Trend and 2008-Liberal scenarios and 2.0 grazing units per ha in the 2008-LTO scenario.

Technological improvements

Milk production per cow in 1998 was 7950 kg with 4.42% fat and 3.46% protein, representing the average production of the Dutch Black-and-White in 1997 (NRS, 1998). For 1998, LW of a mature dairy cow was 625 kg based on estimates from field and experimental data (Devir *et al.*, 1995; Van der Werf *et al.*, 1998; Koenen *et al.*, 1999). As no large-scale data are available for DMIC, for the basic situation DMIC level was simulated for each month from LW and milk production levels (Appendix, equation 2). The DMIC level of a third parity cow in the second month of lactation was considered as a reference value. For 1998, this DMIC level equals 18.5 kg DM/day.

In the period 1993-1997 mean annual increase in milk production was around 110 kg with almost constant fat and protein percentages (NRS, 1998). Milk production in 2008 is therefore set to 9000 kg with current fat and protein percentages. Although no direct selection for increased LW and DMIC is expected, LW and DMIC are higher in 2008 as a result of phenotypic trends for milk production. A phenotypic correlation of 0.20 is assumed between milk production and LW (Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995). Combining this correlation with phenotypic standard deviations for milk production (432 kg; Van der Werf and De Boer, 1989) and LW (50 kg; Koenen and Groen, 1998) results in an approximated LW estimate for 2008 of 650 kg. Also for the basic situation in 2008, DMIC was simulated using milk production and LW levels. The reference DMIC value for 2008 equals 19.8 kg DM/day.

Technological improvements in crop production are expected to increase productivity levels of grass and maize. Net energy production levels for grass for 1998 and 2008 are based on estimates for 1992 assuming an annual increase in efficiency of 1.5% since 1992 (Berentsen *et al.*, 1996). Net energy production levels for maize silage, ground ear silage and fodder beets are based on 1997 (Snoek *et al.*, 1997) assuming a 1% annual increase of production (Berentsen *et al.*, 1996).

Prices of inputs and outputs

Assumed input and output prices in the different scenarios are in Table 4.

For 1998, product prices are based on market prices of 1996/1997. Price of milk (4.42% fat, 3.46% protein) was 0.334 €/kg (Snoek *et al.*, 1997). Two prices for maize were included (Table 4): the first is the price of maize silage including harvesting and transport whereas the second price applies when maize silage is sold standing.

Product prices for scenarios with a moderate price liberalisation (2008-Trend and 2008-LTO) are based on EU policy. In 2008, intervention prices for milk products, beef and cereals are expected to reduce by 15, 30 and 20%, respectively (European Commission, 1998). To reduce unfavourable income effects, plans include compensation for dairy farmers in the Netherlands of € 213 per 5800 kg of milk (European Commission, 1998). Income compensation for the producers of cereals

Table 4. Prices (€) of the main inputs and outputs in the four scenarios.

	1998	2008		
	Actual	Trend	Liberal	LTO
Milk (/kg)	0.334[1]	0.284	0.201	0.284
Culled cows (/kg carcass)	1.86[2]	1.30	0.93	1.30
Male calves (/kg)	3.27[2]	2.29	1.63	2.29
Female calves (/kg)	2.20[2]	1.54	1.10	1.54
Concentrates[3] (/MJ NE_L)	0.0241[2]	0.0228	0.0216	0.0228
Maize silage, purchase (/MJ NE_L)	0.0204[1]	0.0194	0.0183	0.0194
Maize silage, selling (/MJ NE_L)	0.0138[1]	0.0131	0.0124	0.0131

[1] Snoek *et al.*, 1997.

[2] LEI-DLO, 1998b.

[3] Standard concentrate including 7.21 MJ NE_L/kg DM.

cereals is also based on production level (European Commission, 1998). It is expected that the decrease in intervention price of cereals results in lower prices for concentrates, as 50% of the feed stuffs used for concentrates for dairy cows consists of energy sources like grain and grain substitutes (Dubbeldam, 1993). When defining product prices for 2008 for cereals, reduced intervention prices and compensation for cereals are directly combined in product prices. For 2008, assumed product prices for concentrates and maize silage were 5% lower (De Bont and Van Everdingen, 1998).

With full market liberalisation (2008-Liberal scenario), product prices will reduce towards world market levels. Present prices of dairy products at the world market are around 45% lower than prices within the Netherlands (MNLV, 1996). However, the expected higher consumption might increase the milk price (European Commission, 1997; Rabobank, 1998). Therefore, the product price for milk in the scenario 2008-Liberal was set to 65% of the 1998 price. Beef prices in the 2008-Liberal scenario were set to world market prices, equal to 50% of 1998 prices (MLNV, 1996). The decrease in feed prices is expected to be relatively low (10%), as intervention prices for cereals are already close to world market prices (MLNV, 1996).

Farm model

Production circumstances in the four scenarios were implemented in a static linear programming model (Berentsen and Giessen, 1995) that maximises labour income. This model simulates inputs and outputs of a dairy farm for a yearly period. The basic element is a dairy cow, calving in February. Milk production, LW and DMIC from birth until culling are simulated on a monthly basis using the model of Groen (1988). The reference for the simulation of milk production is a first parity cow with a defined 305-day production. Adjustment factors for parity and lactation stage and survival rates are used to calculate average milk production during a cow's lifetime. Live weight is modelled as a function of birth weight, mature LW and age (Appendix, equation 1). The DMIC is modelled as a function of DMIC curves for the basic situation and adjustment factors for lactation stage (Appendix, equation 2). Milk production and LW determine energy and protein requirements. Beef production includes new-born male calves, surplus female calves and disposed cows. A yearly replacement rate of cows by heifers raised on the farm of 25% was assumed.

The feeding strategy was based on energy and protein requirements, DMIC, fill values, structural values and availability of feeds. The fill value of a certain feed indicates the amount of DMIC measured in kg DM of a reference feed that is needed per kg DM of that specific feed (Jarrige *et al.*, 1986). Fill values for concentrates are lower than for roughage but increase at a higher proportion of concentrates in the diet (Jarrige *et al.*, 1986). In winter (November–April), four levels of fill values for concentrates were used in the model. In summer (May–October), only the lowest fill value for concentrates was used, as the amount of concentrates fed in summer is generally small. The structural value represents the proportion of structural material per kg of the feed. The average structural value of the diet should be at least one third (CVB, 1997). Energy and protein content, structural value and fill value of the available feeds are in Table 5. Energy content of grass and grass silage is affected by the level of nitrogen fertiliser which ranges from 100 to 500 kg N/ha/year. Three different concentrates were available for dairy cows: standard concentrates, low-protein concentrates and high-protein concentrates. Dried beet pulp and ground ear silage can be used to substitute concentrates. Availability of some feeds was restricted: fresh grass was only available in summer, whereas grass silage and fodder beets were only available in winter. In summer, the diet must include at least 1 kg of concentrates, whereas in winter it must include at least 2 kg DM of grass silage. Concentrates and maize silage can be purchased, whereas grass, maize and fodder beets can be produced on farm. Maize can be harvested as whole plant silage or as ground ear silage (grains, the cob, the husks and the shank of the maize plants). Costs at farm level include fixed and variable costs. Fixed costs include interest, costs of depreciation and maintenance of machinery and milking parlour (total 31,023 €) and costs of land (277 €/ha). Costs of land are considered fixed, as a change in the available land area was not considered within a scenario. Housing costs were variable and based on the number of places in the barn (309 €/place). The number of animals also determines other variable costs (health care, breeding and energy for milking). These costs were 281 € per cow and 212 € per unit of young stock

Table 5. Energy and protein content, structural value and fill value of feeds supplied.

	Energy content (MJ NE_L/kg DM)	Protein content (DVE/kg DM)	Structural value	Fill value (kg DM/kg DM)
Grass[1]	6.66-6.93	0.093-0.105	0.55	1.00
Grass silage[1]	5.80-6.07	0.065-0.075	0.90	1.08
Maize silage	6.21	0.047	0.60	1.13
Dried beet pulp	7.12	0.110	0.00	0.28
Ground ear silage	7.74	0.062	0.00	0.60
Fodder beets	6.25	0.074	0.00	0.60
Concentrates	6.90-7.20	0.089-0.200	0.00	0.28-0.70

[1] Level of nitrogen fertiliser ranged from 100 to 500 kg/ha/year.

(1 calf and 0.96 growing heifer). Costs for the production of maize and fodderbeets (excluding fertiliser) were 1144 and 2234 €/ha, respectively. Labour costs were not considered explicitly in the model, but costs of additional labour are 15 €/h when total labour required exceeds 3028 h.

Derivation of economic values

To estimate the effect of genetic improvement, management factors were varied to maximise labour income before and after a 1% increase in the level of a trait while keeping all other traits constant. The parameters that were changed were mature LW and DMIC of a reference feed (Jarrige *et al.*, 1986) of a third parity cow in the second month of lactation. Changes in these parameters also changed LW and DMIC at other stages of life. By using simulated DMIC curves from the basic situations (Appendix, equation 3) DMIC was explicitly kept constant when LW or FPCM were varied. Economic values for LW and DMIC are estimated comparing labour income of the optimised farm before and after the genetic change and are expressed per cow and per unit of genetic change.

Two analyses tested the effect of model assumptions on estimated EVs in the 2008-Trend scenario. In the first analysis, production intensity is varied by changing the area of land by 10 ha at a constant total milk production. In the second analysis, genetic levels for LW, DMIC and milk production are independently varied by 10 and 20%.

RESULTS

Farm characteristics

Optimised farm characteristics in each scenario are in Table 6. Milk quota restricts maximisation of labour income in all scenarios, except for the 2008-Liberal scenario. In all scenarios in 2008, legislation on phosphate surpluses also affects maximisation of labour income. Availability of own labour affects labour income only in the 2008-Liberal scenario. Maximum stocking density did not affect labour income in any scenario investigated.

In the 1998-Actual scenario, the dairy herd comprises 49.1 cows and 13.9 units of young stock. Land is used for the production of grass (23.0 ha) and maize silage (10.0 ha). A small surplus of maize silage (1.6 ha) is sold. Nutrient surpluses are 144 and –2.5 kg/ha for nitrogen and phosphate, respectively. The phosphate surplus is low as phosphate input through fertiliser (27.5 kg/ha) is not included in the legislation before 2000 (MNLV, 1997).

In the 2008-Trend scenario, the optimised farm comprises 53.3 cows and 15.1 units of young stock. Compared to 1998, the increase in number of cows is relatively less than the increase in milk quota because of increased production levels per cow. This results in a lower stocking density (1.57 grazing units/ha), at similar production intensity (12,000 kg/ha). Nitrogen surpluses are acceptable, whereas phosphate was in surplus by 2.8 kg/ha.

In the 2008-Liberal scenario (no milk quota), number of cows is restricted by the availability of produced grass and maize silage. The 71.6 cows increase milk output and stocking density by about 35% compared to the 2008-Trend scenario. Total labour demand exceeds the availability of own labour by 438 h.

Nitrogen and phosphate inputs increase due to higher input of concentrates and fertilisers. Nitrogen surpluses are below maximum, but phosphate surpluses

Table 6. Farm characteristics in the four scenarios.

	1998	2008		
	Actual	Trend	Liberal	LTO
Cattle				
No. lactating cows	49.1	53.3	71.6	53.3
No. young stock (units)	13.9	15.1	20.3	15.1
Stocking density (gu/ha)[1]	1.75	1.57	2.11	1.57
Milk production (kg)	390,000	480,000	644,122	480,000
Intensity (kg milk/ha)	11,818	12,000	16,103	12,000
Labour (h)	2776	2902	3466	2991
Grass production				
Grass land (ha)	23.0	21.8	29.3	25.3
Nitrogen use (kg/ha)	284	307	307	195
Maize production (ha)				
On farm use	8.4	8.0	10.7	8.1
For sale	1.6	10.2	0.0	0.0
Ground ear silage	0.0	0.0	0.0	4.5
Nitrogen balance (kg/ha)				
Input	237	236	267	153
Output	93	113	118	82
Surplus[2]	144 (262)	123 (144)	149 (159)	71 (151)
Phosphate balance (kg/ha)				
Input	31.6	69.4	62.4	49.3
Output	34.1	46.6	38.9	29.0
Surplus[2]	–2.5 (40)	22.8 (20)	23.5 (20)	20.3 (20)

[1] gu = grazing units.

[2] Acceptable surpluses within brackets.

exceed the maximum level by 3.5 kg/ha.

In the 2008-LTO scenario, the number of cows is equal to the 2008-Basic scenario, but more land is used for grass production and less is used to produce maize; 4.5 ha maize is harvested as ground ear silage. The exclusion of selling maize silage reduces options for economical land use compared to the 2008-Trend scenario and therefore 2.1 ha of land is laid fallow. The low level of fertiliser use reduces nitrogen and phosphate inputs. Realised nitrogen surpluses are low (71 kg/ha) whereas phosphate surpluses slightly exceed the acceptable level.

Composition of the feeding rations in summer and winter in each scenario are in Table 7. In summer, rations mainly include grass and are supplemented by concentrates or dried beet pulp. In the scenarios for 2008, concentrates are largely replaced by dried beet pulp, which can be profitable under stringent environmental legislation. Dried beet pulp is slightly more expensive than concentrates but has lower nitrogen and phosphate contents (Berentsen and Giessen, 1995). In summer, energy requirements and DMIC restrict the rations.

In winter, the rations include grass and maize silage supplemented by concentrates or ground ear silage. No scenario uses more than 2.0 kg DM of grass silage. The 2008-Liberal scenario includes the largest proportion of concentrates. Only in the 2008-LTO scenario ground ear silage is included. In winter, rations are restricted by energy and protein requirements in all scenarios, whereas DMIC is also restricting in the 1998-Actual, 2008-Basic and 2008-LTO scenarios.

Table 7. Daily feeding rations in summer and winter period in the four scenarios.

	1998	2008		
	Actual	Trend	Liberal	LTO
Summer ration				
Grass (kg DM)	16.68	17.48	17.48	17.40
Concentrates (kg)	2.39	0.00	0.00	0.00
Dried beet pulp (kg DM)	0.00	3.12	3.12	3.38
Restrictions[1]	E, D	E, D	E, D	E, D
Winter ration				
Grass silage (kg DM)	2.00	2.00	2.00	2.00
Maize silage (kg DM)	8.49	10.59	8.14	8.35
Concentrates (kg)	6.09	5.65	8.02	3.37
Ground ear silage (kg DM)	0.00	0.00	0.00	3.71
Restrictions[1]	E, P, D	E, P, D	E, P	E, P, D

[1] Ration can be restricted by energy requirements (E), protein requirements (P) and dry-matter intake capacity (D).

The economic results for each scenario are in Table 8. In the 1998-Actual scenario, 90% of total returns originate from milk production, 9% from beef production and less than 1% from the sale of maize silage. From Table 8 it appears that fixed costs and costs for housing are the most important costs. Labour income is 31,892 €. In the 2008-Trend scenario, total returns are 32,443 € higher than in the 1998-Actual scenario, which mainly originates from higher milk production, lower beef production and the introduction of a compensation scheme. The higher total costs are mainly related to maize production, concentrates and housing. Costs now also include a levy of 257 € for phosphate surpluses. Labour income is 45,711 €. In the 2008-Liberal scenario, total returns are 25,443 € lower than in the 2008-Trend scenario. The effect of lower prices for milk and beef on total returns can not be compensated by increased milk and beef production. The larger number of cows increases costs for concentrates and housing. Labour income is reduced to –2367 €. In the 2008-LTO scenario, returns from milk and beef production are the

Table 8. Economic results (€/year) in the four scenarios.

	1998	2008		
	Actual	Trend	Liberal	LTO
Returns				
Milk	130,429	136,449	140,021	136,449
Beef	13,286	11,579	12,566	11,579
Sold maize	1,872	12,374	0	0
Compensation	0	17,628	0	17,628
Total returns	145,587	178,030	152,587	165,656
Variable costs				
Grass production	6,059	6,103	8,190	6,248
Maize production	8,861	15,235	9,719	11,430
Concentrates[1]	13,269	18,128	23,061	12,786
Fertiliser	3,656	5,052	4,245	2,709
Hired labour	0	0	6,365	0
Housing	22,922	24,920	33,440	24,920
Levy	0	257	319	27
Other	18,770	20,529	27,520	20,529
Fixed costs	40,158	42,095	42,095	42,095
Total costs	113,695	132,319	154,954	120,744
Labour income	31,892	45,711	-2,367	44,912

[1] Including dried beet pulp.

same as in the 2008-Trend scenario. However, total returns are lower as the sale of maize silage is no longer an option. Reduced returns are partly compensated by lower costs for maize production and fertiliser. Labour income is 44,912 €, about 2% lower than in the 2008-Trend scenario.

Economic values

Table 9 specifies changes in returns and costs when the genetic level of LW or DMIC is increased by 1% in the four scenarios. When LW is increased in the 1998-Actual scenario, more concentrates are included in the diet to replace grass (summer) or maize silage (winter). Concentrate input per cow increases by about 31 kg/year. A higher LW results in increased returns from beef and maize production. Total costs increase mainly by higher costs for concentrates. The resulting EV for LW is –0.17 €/kg/cow/year (–50.66 €/6.25 kg/49.1 cows).

When DMIC increases, concentrates input can be decreased by about 97 kg/cow/year by substitution with cheaper grass and maize silage. A higher DMIC reduces returns maize sales as more maize silage is consumed. Total costs are mainly reduced by a lower input of concentrates. The EV for DMIC in the 1998-Actual scenario is 33 €/kg/cow/year.

In the 2008-Trend scenario, the EV for LW is more negative than in the 1998-Actual scenario. This is caused by lower beef returns and higher marginal feed costs as a result of the inclusion of ground ear silage in the diet. When LW increases, produced maize is partly harvested as ground ear silage. Total maize production increases but the amount of maize silage used on farm or sold is lower. The higher productivity of grass and maize production decreases the costs of roughage which results in a higher EV for DMIC, compared to the 1998-Actual scenario.

In the 2008-Liberal scenario, higher levels for LW and DMIC are associated with small changes in the number of cows (+0.06 and –0.69, respectively) which affect many returns and costs. Total returns from milk and beef production increase with LW. Total costs increase by higher costs for concentrates and higher variable costs due to the higher number of cows. The EV of LW (–0.29 €/kg/cow/year) was lower than in other scenarios, mainly because of much lower beef prices. A higher DMIC results in a reduction in the number of cows and reduces total returns by 1,484 €/year. Total costs are largely reduced by lower costs for concentrates. The EV of DMIC (18 €/kg/cow/year) is much lower than in other scenarios as DMIC is only limiting in summer (Table 7).

In the 2008-LTO scenario, a higher LW results in higher beef returns and higher costs for concentrates. The EV for LW of –0.19 €/kg/cow/year is less negative than in the 2008-Trend scenario.

Table 9. Changes in returns and costs (€/year) and economic values (€/kg/cow/year) after increasing live weight (LW) and dry-matter intake capacity (DMIC) by 1% in the four scenarios.

	1998-Actual		2008					
			Trend		Liberal		LTO	
	LW	DMIC	LW	DMIC	LW	DMIC	LW	DMIC
Returns								
Milk	0.00	0.00	0.00	0.00	99.12	–1362.02	0.00	0.00
Beef	105.02	0.00	85.53	0.00	94.02	–122.24	85.53	0.00
Maize	68.46	–534.89	–32.89	–675.85	0.00	0.00	0.00	0.00
Total returns	173.48	–534.89	52.64	–675.85	193.14	–1484.26	85.53	0.00
Costs								
Grass production	–4.71	55.76	–4.11	63.11	28.52	4.20	–4.16	63.75
Maize production	12.85	–181.69	20.67	–197.03	–9.56	–94.54	63.76	–66.37
Fertiliser	0.66	–19.81	–4.46	–29.34	93.77	13.05	3.53	30.81
Concentrates	215.34	–690.01	113.12	–906.59	122.36	–821.65	82.48	–460.68
Housing	0.00	0.00	0.00	0.00	23.67	–325.28	0.00	0.00
Labour	0.00	0.00	0.00	0.00	34.40	–246.52	0.00	0.00
Levy phosphate	0.00	0.00	2.30	3.75	5.49	1.24	4.82	12.53
Other	0.00	0.00	0.00	0.00	28.39	–267.76	0.00	0.00
Total costs	224.14	–835.75	127.52	–1066.10	327.04	–1737.26	150.43	–419.96
Net effect	–50.66	300.86	–74.88	390.25	–133.90	253.00	–64.90	419.96
Economic value	–0.17	33	–0.22	37	–0.29	18	–0.19	40

With higher DMIC, the area of grassland increases and all 40 ha are now used. A higher DMIC has no effect on returns but reduces total costs by 420 € which results in an EV for DMIC of 40 €/kg/cow/year.

Sensitivity analysis

Economic values for LW and DMIC for farms with low and high milk production intensities are in Table 10. At low production intensity (land area is increased by 10 ha) more land is available to produce roughage. In the 1998-Actual and 2008-Trend scenarios, the additional area of land is used to produce maize silage for the market. In the 2008-Liberal scenario, the production of maize, grass and milk is increased by exactly 25%. In the 2008-LTO scenario, the area of unused land is increased by 10 ha. Not withstanding these changes, at a low intensity marginal costs for roughages and concentrates are the same as in the situation with an average intensity which explains the unchanged EVs.

At high production intensity (land area is decreased by 10 ha), farms in the 1998-Actual, 2008-Trend and 2008-Liberal scenarios purchase maize silage. Under production circumstances with purchased maize silage, marginal costs of roughage are higher than in situations with only home-produced maize silage. At constant costs for concentrates, the increased roughage costs imply a less negative EV for LW as the value of saved roughage is higher. In the 2008-LTO scenario, restrictions on stocking density reduce the number of cows. Farms in this scenario have to feed the cows with home-grown concentrates or imported concentrates. Marginal costs of roughage increase as all land has to be used for crop production. In this intensive situation additional energy requirements are largely covered by the import of concentrates which decreases the EV for LW. In all scenarios, increased marginal costs for roughage reduce the difference in costs between concentrates and roughage

Table 10. Economic values (€/kg/cow/year) for live weight (LW) and dry-matter intake capacity (DMIC) for farms with a low and high production intensities in each of in the four scenarios.

	1998	2008		
	Actual	Trend	Liberal	LTO
Low production intensity (10 ha increase in land area)				
LW	–0.17	–0.22	–0.29	–0.19
DMIC	33	37	18	40
High production intensity (10 ha decrease in land area)				
LW	–0.10	–0.22	–0.14	-0.22
DMIC	16	29	13	35

and result consequently in lower EVs for DMIC.

Estimated EVs for various levels of LW, DMIC and milk yield in the 2008-Trend scenario are in Table 11. When assumed LW deviates from the 2008-base level (650 kg), energy and protein requirements and beef production change, whereas DMIC and milk yield remain constant. The increase in requirements was larger for energy than for protein: e.g. increasing LW from 520 to 780 kg increased energy requirements and protein requirements by 11 and 2%, respectively. The EVs for LW and DMIC with increasing LW levels do not show a consistent pattern. One explanation might be different effects of increased energy and protein levels on the diet in winter. When LW increases, the use of maize silage is reduced, whereas the total amount of concentrates increases. Up to LW levels of 650 kg, the amount of high protein concentrates decreases, whereas the amount of standard concentrates increases. But at higher LW levels, ground ear silage is included in the diet which minimises changes in concentrates with increased LW. At low LW levels the amount of sold maize silage increases with increases in LW, whereas it decreases at higher LW levels. For DMIC, estimated EVs tend to increase with higher LW as increased maintenance requirements at constant DMIC result in rations with higher energy densities.

Table 11. Economic values for live weight (LW) and dry-matter intake capacity (DMIC) in the 2008-Trend scenario when levels for LW, DMIC and milk yield (MY) are independently varied.

		Economic value (€/kg/cow/year)	
Trait	Level	LW	DMIC
LW (kg)	520	–0.25	35
	585	–0.29	37
	715	–0.22	36
	780	–0.19	36
DMIC (kg DM/day)	15.81	n.a.[1]	n.a.[1]
	17.78	–0.28	37
	21.74	–0.01	6
	23.71	0.06	0
MY (kg/year)	7200	0.00	2
	8100	–0.16	25
	9900	–0.21	36
	10,800	–0.28	46

[1] Not available.

Assumed DMIC levels largely affect the EVs for LW and DMIC. When DMIC is 20% lower than in the in base situation, no feasible solution can be obtained. When DMIC is 10% lower, ground ear silage is included in the diet, which increases marginal feed costs. The EV for LW decreases to –0.28 €/kg/cow/year, whereas the EV for DMIC increases to 37 €/kg/cow/year. At high DMIC levels, the proportion of concentrates in the diet can decrease greatly which results in lower marginal feed prices. At higher DMIC, the EV of LW increases whereas the EV for DMIC decreases. At DMIC levels of 23.71 kg DM/day or higher the EV for DMIC is zero as DMIC no longer restricts the ration.

Level of milk production has a considerable effect on the EVs of LW and DMIC. At milk production level of 7200 kg, small amounts of concentrates are used. The EV for LW is zero, whereas the EV for DMIC is only slightly positive. At milk production levels ≥9900 kg, ground ear silage is included in the diet in winter. At high production levels, marginal feed costs increase which result in more negative EVs for LW and more positive EVs for DMIC.

DISCUSSION

Optimisation goals

The aim of this study was to evaluate the effect of genetic change in LW and DMIC on labour income of a dairy farmer. These effects were estimated by comparing labour income with optimal management before and after genetic improvement, which ignores possible effects of changes in labour input of the farmer. Maximising profit, i.e. explicitly considering costs for own labour and management, might change optimal farm plans as labour input is required for home-grown roughages but not for purchased concentrates. Therefore, profit was also maximised for two scenarios: scenario 2008-Liberal, which included most labour input and scenario 2008-LTO which had the highest EV for DMIC. When costs of all labour input were set to 15 €/h, EVs were unchanged in the 2008-Liberal scenario. In the 2008-LTO scenario, EVs for LW and DMIC slightly changed to –0.22 and 37 €/kg/cow/year, respectively.

In practical situations, the optimisation goal might be less clear. When labour income is already high, marginal returns from increased labour input can have a lower value for a dairy farmer than in a situation with a low labour income (Zachariasse, 1972). This implies that in some situations activities with a lower labour input that do not maximise labour income might be preferred.

Production circumstances

Increased profitability after genetic improvement results from saved input factors or lower costs for production factors. The net effect on labour income is determined by the amount and value of changed production factors. The marginal value of saved production factors corresponds to their actual use in the enterprise they are saved from (Groen, 1989c). In this study, EVs were estimated under production circumstances that varied in product prices, production levels and production circumstances. This variation should be considered when current estimates for EVs are compared with literature estimates.

In the study of Groen (1989b), marginal costs of both concentrates and roughages were set to market prices. Estimated EVs for LW in that study were more negative than in the present study, which might be caused by overestimating actual marginal costs for roughages. A smaller difference between marginal costs for concentrates and roughages might also have resulted in lower EVs for DMIC in the study of Groen and Korver (1989).

Both the 2008-Liberal scenario and the study of Visscher *et al.* (1994) assumed low prices for milk and beef in the absence of milk quota. However, in the study of Visscher *et al.* (1994), in production circumstances whereby total feed input was restricted, the EV for LW was more negative than obtained in the 2008-Liberal scenario. With a fixed feed input, the increased total energy requirements result in a reduced number of cows which reduces total milk production.

Combined selection

When deriving EVs, it was assumed that the breeding goal included all traits affecting labour income. This means that costs for health and fertility are assumed to be constant at different levels for LW and DMIC. This assumption is appropriate in deriving EVs for breeding goal traits. As a result of phenotypic and genetic correlations, higher levels of DMIC might indirectly decrease costs for health and fertility. In early lactation, many high producing cows are unable to consume enough feed to meet energy and protein demands and are therefore in a negative energy balance (Gravert, 1985). Unfavourable phenotypic correlations are reported between size and duration of the negative energy balance and health and fertility (e.g. Villa-Godoy *et al.*, 1988; Spicer *et al.*, 1990; Zurek *et al.*, 1995). While the derivation of EVs for weighting traits in the breeding goal excludes them, the phenotypic and genetic correlations between traits should be properly considered in deriving the selection-index regression factors.

With direct selection for milk only, correlated responses in DMIC will be positive, but not large enough to cover the increased energy requirements without increasing the energy density of the diet (Van Arendonk *et al.*, 1991). With direct selection for milk only, also correlated responses in LW will be positive; cows will become larger. Combined selection on milk production, LW and DMIC will change genetic trends relative to direct selection for milk only. Steverink *et al.* (1994b) suggested that a combined selection strategy still resulted in an increased LW, but that the response in LW was substantially smaller than in situations without LW in the breeding goal. This study was limited to the derivation of EVs; research into the relevance of recording LW and DMIC requires investigation into discounting of EVs, estimates for the genetic and phenotypic (co)variances on all traits and assumptions on selection intensities and numbers of records available for breeding value estimation for selection candidates (e.g. Groen, 1990).

The practical application of the estimated EVs from this study is complicated by uncertainty about the realisation of the described scenarios. This uncertainty needs to be considered when developing breeding strategies. On the one hand, incorrectly chosen EVs may result in (according to realised future circumstances) non-optimal genetic trends (resulting from predicted future circumstances). This loss in efficiency depends on the relative EV of the trait within the breeding goal (Smith, 1983). Groen (1990) showed that in a breeding goal including LW, DMIC and milk production the effect of incorrectly estimated EVs for LW and DMIC on efficiency of within-breed selection might be small as milk production traits are likely to dominate the selection index. On the other hand, competitive positions of individual breeding organisations enforce the choice of EVs to be as precise as possible. Defining future scenarios for agricultural production and deriving EVs of genetic improvement for these scenarios is a useful tool in developing breeding strategies that are robust to changes in markets and politics.

REFERENCES

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Berentsen, P.B.M. and G.W.J. Giessen, 1995. An environmental-economic model at farm level to analyse institutional and technical change in dairy farming. *Agric. Syst.* 49: 153-175.

Berentsen P.B.M. and G.W.J. Giessen, 1996. *The effect of sustainability requirements on the economic value of dry-matter intake capacity.* Pages 128-130 *in:* Groen, A.F. and J. Van Bruchem (Eds.). Utilization of local feed resources by dairy cattle. EAAP Publication no. 84. Wageningen Pers. Wageningen, The Netherlands.

Berentsen, P.B.M., Giesen, G.W.J. and J.A. Renkema, 1996. Scenarios of technical and institutional change in Dutch dairy farming. *Neth. J. Agric. Sci.* 44: 193-208.

CVB, 1997. *Voedernormen landbouwhuisdieren en voederwaarde veevoeders.* Centraal Veevoederbureau. Lelystad, The Netherlands. 104 pp.

De Bont, C.J.A.M. and W.H. Van Everdingen, 1998. Agenda 2000: Inkomens rundveehouders en fabrieksaardappeltelers onder vuur. *Agri-monitor* 4: 1-3.

Dempfle, L., 1989. *Increasing the efficiency of the dairy cow with regard to body size.* Research bulletin 4. Livestock Improvement Corporation. Hamilton, New Zealand. 24 pp.

Devir, S., Zur, B., Maltz, E., Genizi, A. and A. Antler, 1995. A model for the prediction of dairy cow body weight based on a physiological timescale. *J. Agric. Sci. Cambr.* 125: 415-424.

Dubbeldam, R.R., 1993. *Annual statistics of feedstuffs 1987/88, 1988/89 and 1989/90.* Periodical report 65 – 87/90. Agricultural Economic Research Institute. The Hague, The Netherlands. 99 pp.

European Commission, 1991. *Council directive (91/676/EEC) of 12 December 1991 concerning the protection of waters against pollution caused by nitrates from agricultural sources.* European Commission. Brussels, Belgium. 8 pp.

European Commission, 1997. *Situation and outlook dairy sector. CAP 2000.* Working document. European Commission. Brussels, Belgium. 60 pp.

European Commission, 1998. *Proposals for council regulations (EC) concerning the reform of the common agricultural policy.* COM(98) 158-final. Brussels, Belgium.

Gravert, H.O., 1985. Genetic factors controlling feed efficiency in dairy cows. *Livest. Prod. Sci.* 13: 87-99.

Groen, A.F., 1988. Derivation of economic values in cattle breeding. A model at farm level. *Agric. Syst.* 27: 195-213.

Groen, A.F., 1989a. *Cattle breeding goals and production circumstances.* Ph.D. Thesis. Wageningen Agricultural University. Wageningen, The Netherlands. 167 pp.

Groen, A.F., 1989b. Economic values in cattle breeding. I. Influences of production circumstances in situations without output limitations. *Livest. Prod. Sci.* 22: 1-16.

Groen, A.F., 1989c. Economic values in cattle breeding. II. Influences of production circumstances in situations with output limitations. *Livest. Prod. Sci.* 22: 17-30.

Groen, A.F., 1990. Influences of production circumstances on the economic revenue of cattle breeding programmes. *Anim. Prod.* 51: 469-480.

Groen, A.F. and S. Korver, 1989. The economic value of feed intake capacity of dairy cows. *Livest. Prod. Sci.* 22: 269-281.

Groen, A.F., Steine, T., Colleau, J.-J., Pedersen, J., Pribyl, J. and N. Reinsch, 1997. Economic values in dairy cattle breeding, with special reference to functional traits. Report of an EAAP-working group. *Livest. Prod. Sci.* 49: 1-21.

Harris, B.L., 1998. Breeding dairy cattle for economic efficiency: a New Zealand pasture-based system. *Proc. 6th World Congr. Genet. Appl. Livest. Prod.* 25: 383-386.

Harris, D.L., 1970. Breeding for efficiency in livestock production: defining the economic objectives. *J. Anim. Sci.* 30: 860-865.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 17-25.

Jarrige, R. Demarquilly, C., Dulphy, J.P., Hoden, A., Robelin, J., Beranger, C., Geay, Y., Journet, M., Malterre, C., Micol, D. and M. Petit, 1986. The INRA "fill unit" system for predicting the voluntary intake of forage-based diets in ruminants: a review. *J. Anim. Sci.* 63: 1737-1758.

Koenen, E.P.C. and A.F. Groen, 1998. Genetic evaluation of body weight of lactating

Holstein heifers using body measurements and conformation traits. *J. Dairy Sci.* 81: 1709-1713.

Koenen, E.P.C., Groen, A.F. and N. Gengler, 1999. Phenotypic variation in live weight and live-weight changes of lactating Holstein-Friesian cows. *Anim. Sci.* 68: 109-114.

Köhne, M., 1968. Die Leitungssteigerung in der Tierproduktion aus der Sicht der Betriebswirtschaft. *Züchtungsk.* 40: 393-409.

LEI-DLO, 1998a. *Bedrijfsuitkomsten in de Landbouw 1993/1994-1996/1997.* Landbouw-Economisch Instituut. The Hague, The Netherlands.

LEI-DLO, 1998b. *Land- en tuinbouwcijfers 1998.* Landbouw-Economisch Instituut. The Hague, The Netherlands. 295 pp.

LTO, 1998. *Uitzicht op een veelzijdige toekomst. De visie van LTO Nederland op de toekomst van de melkveehouderij in Nederland.* LTO. The Hague, The Netherlands. 36 pp.

MLNV, 1996. Gemeenschappelijk landbouwbeleid op langere termijn. MNLV. The Hague, The Netherlands. 33 pp.

MLNV, 1997. Gewijzigde Meststoffenwet. *Staatsblad,* 360.

NRS, 1998. *Jaarstatistieken 1997.* Nederlands Rundvee Syndicaat. Arnhem, The Netherlands. 62 pp.

Rabobank, 1998. *Toekomst voor een veelzijdige melkveehouderij.* Rabobank Nederland. Eindhoven, The Netherlands. 54 pp.

Smith, C., 1983. Effects of changes in economic weights on the efficiency of index selection. *J. Anim. Sci.* 56: 1057-1064.

Snoek, H., Hemmer, H., Van Brakel, C., Ellen, H., Ingelaat, F. and L. Westerlaken, 1997. *Kwantitatieve informatie Veehouderij 1997-1998.* Praktijkonderzoek Rundvee, Schapen en Paarden. Lelystad, The Netherlands. 398 pp.

Spicer, L.J., Tucker, W.B. and G.D. Adams, 1990. Insulin-like growth factor-I in dairy cows: relationships among energy balance, body condition, ovarian activity and estrous behavior. *J. Dairy Sci.* 73: 929-937.

Steverink, M.H.A., Groen, A.F. and P.B.M. Berentsen, 1994a. The influence of environmental policies for dairy farms on dairy cattle breeding goals. *Livest. Prod. Sci.* 40: 251-261.

Steverink, M.H.A., Van Arendonk, J.A.M., Berentsen, P.B.M. and A.F. Groen, 1994b. *Gecombineerde selectie op melkproductiekenmerken en lichaamsgewicht.* Report Department of Animal Breeding, Wageningen Agricultural University. Wageningen, The Netherlands. 32 pp.

Van Arendonk, J.A.M., Nieuwhof, G.J., Vos, H. and S. Korver, 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. *Livest. Prod. Sci.* 29: 263-275.

Van der Werf, J.H.J. and W. De Boer, 1989. Estimation of genetic parameters in a crossbred population of Black and White dairy cattle. *J. Dairy Sci.* 72: 2615-2623.

Van der Werf, J.H.J., Van der Waaij, E.H., Groen, A.F. and G. De Jong, 1998. An index for beef and veal characteristics in dairy cattle based on carcass traits. *Livest. Prod. Sci.* 54: 11-20.

VanRaden, P.M., 1988. Economic value of body size in Holsteins. *J. Dairy Sci.* 71 (Suppl. 1): 238.

Veerkamp, R.F., 1996. *Live weight and feed intake in dairy cattle breeding.* Pages 173-180 *in* Proc. Int. workshop on Genetic Improvement of Functional Traits in cattle (GIFT).

INTERBULL bulletin nr. 12. INTERBULL. Uppsala, Sweden.

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.

Villa-Godoy, A., Hughes, T.L., Emery, R.S., Chapin, L.R. and R.L. Fogwell, 1988. Association between energy balance and luteal function in lactating dairy cows. *J. Dairy Sci.* 71: 1063-1072.

Visscher, P.M., Bowman, P.J. and M.E. Goddard, 1994. Breeding objectives for pasture based dairy production systems. *Livest. Prod. Sci.* 40: 123-137.

Zachariasse, L.C., 1972. *Analyse van het vraagstuk der uiteenlopende rentabiliteit van vergelijkbare agrarische bedrijven.* Ph.D. Thesis. Landbouwhogeschool. Wageningen, The Netherlands. 67 pp.

Zeddies, J., 1992. *Die wirtschaftliche Bedeutung der Leistungsmerkmale beim Rind.* University of Hohenheim. Stuttgart, Germany. 61 pp.

Zurek, E., Roxcroft, G.R. and J.J. Kennelly, 1995. Metabolic status and interval to first ovulation in postpartum dairy cows. *J. Dairy Sci.* 78: 1909-1920.

APPENDIX

Age-dependent LW is modelled by:

$$\mathrm{LW} = A\,[1 - (1 - (\mathrm{BW}/A)^{1/3})\, e^{-0.0028\,t}]^3 \qquad (1)$$

where

A = mature LW (kg),

BW = birth weight (kg) and

t = age (days).

Dry-matter intake capacity (kg DM/day) of a reference feed in the *i*th month of the *j*th lactation in the basic situation is given by:

$$\mathrm{DMIC}_{ij} = 0.90\,\{[0.135\,\mathrm{LW}_j^{0.75} + 0.20\,(\mathrm{FPCM}_j - 5000/305)]\,\mathrm{DMIM}_i + 0.20(\mathrm{FPCM}_{ij} - \mathrm{FPCM}_j)\} \qquad (2)$$

where

LW_j = age-dependent LW (kg),

FPCM_j = mean fat-and-protein corrected milk production during lactation *j* (kg/day),

FPCM_{ij} = mean fat-and-protein corrected milk production in month *i* and lactation *j* (kg/day) and

DMIM_i = multiplicative adjustment factor for month *i* in lactation on DMIC.

The fat-and-protein-corrected milk production is a function of mean milk production and multiplicative adjustment factors for the effects of parity and lactation stage.

To vary DMIC as a genetic trait independently from LW and fat-and-protein corrected milk production, DMIC in alternative situations was derived by changing the DMIC levels from the basic situations as a function of the defined change in DMIC (ΔDMIC) for a third parity cow in the second month of lactation and multiplicative adjustment factors for month in lactation:

$$\mathrm{DMIC}_{ij} = \mathrm{DMIC}_{ij}(\text{basic situation}) + \Delta\mathrm{DMIC} * (\mathrm{DMIM}_i/\mathrm{DMIM}_2) \qquad (3)$$

CHAPTER 9

General discussion

This thesis is on the feasibility and relevance of selection for body weight (BW) in dairy cattle.

The first aim of this thesis was to study procedures of data recording for a genetic evaluation for BW. Ideally, such observations can be measured early in life, have a high heritability and a high genetic correlation with the trait to be improved. To evaluate the suitability of BW observations for a genetic evaluation, statistical parameters for BW such as adjustment factors, repeatabilities and heritabilities were estimated. The implications of these estimates for a large-scale genetic evaluation for BW are discussed in the first section of this chapter.

The second aim of this thesis was to study the relevance of considering estimated breeding values (EBVs) for BW when making selection decisions. Selection for BW might not only affect BW levels but, due to genetic correlations, it might also affect dry-matter intake capacity (DMIC) and body condition score (BCS) levels. Therefore, this thesis also estimated genetic parameters for DMIC and BCS. Possibilities for a genetic evaluation for these traits are discussed in the second section of this chapter.

The estimates for the genetic parameters and economic values (EVs) of BW from this thesis are useful to compare alternative selection strategies. The effects of selection strategies with and without additional information on BW are evaluated in the third section of this chapter.

Finally, the main conclusions of this thesis are presented in the fourth section of this chapter.

GENETIC EVALUATION FOR BODY WEIGHT

Data recording

The main motivation for selection for BW is to account for the genetic variation in maintenance requirements during life. To optimise data recording systems for BW, estimates for the means and correlations between BW during life are helpful. Ideally, a study on BW observations during life includes repeated observations on many animals for a period of years. However, due to practical reasons, such data are seldom available. For this reason, estimates for mean BW at various ages were in this thesis mainly based on data from small-scale experiments with BW recorded during a limited period of time.

The BW observations on growing heifers showed that mean BW increased from about 40 kg at birth to 508 kg after first calving (Chapter 2). The analysis of BW of lactating cows (Chapter 3) illustrated that cows were still growing until the end of third lactation: mean BW increased from 537 kg after first calving to 633 kg after third calving. In Chapter 2, mature BW was predicted by extrapolating two mathematical functions that were fitted to BW data until first calving. Although the Von Bertalanffy and the two-phase logistic function were fitted to the same data, predicted mature BW was very different for both functions (667 *vs*. 546 kg). Unfortunately, the number of BW observations after first calving was too small to validate these extrapolations adequately. As BW observations on fourth or higher parities were not available, a more detailed analysis of mature BW was not feasible.

The estimated growth patterns for BW from this thesis can indirectly be compared to carcass weights of cows at different ages. Figure 1 shows the mean carcass weights of culled Dutch Holstein-Friesian cows and suggests that cows are still growing up to the age 60 months (about the end of third parity) which is in line with the results of Chapter 3. Assuming a fixed dressing percentage of 47% (Liinamo *et al*., 1999), BWs at 24 months (first calving), 36 months (second calving), 48 months (third calving) and ≥60 months (fourth calving and later) are predicted to be 560, 595, 625 and 635 kg, respectively. These estimates suggest that BW at first calving already represents 88% of mature BW, which was higher than the estimate of 80% of Groen (1988). Based on carcass weights, predicted mean BW during first and second lactation was about 91 and 97% of the mean BW during third lactation, respectively. These estimates are higher than the estimates from Chapter 3 (85 and 92%). Also Hietanen and Ojala (1995) found somewhat lower proportions (87 and 95%). The relative higher estimates for BW

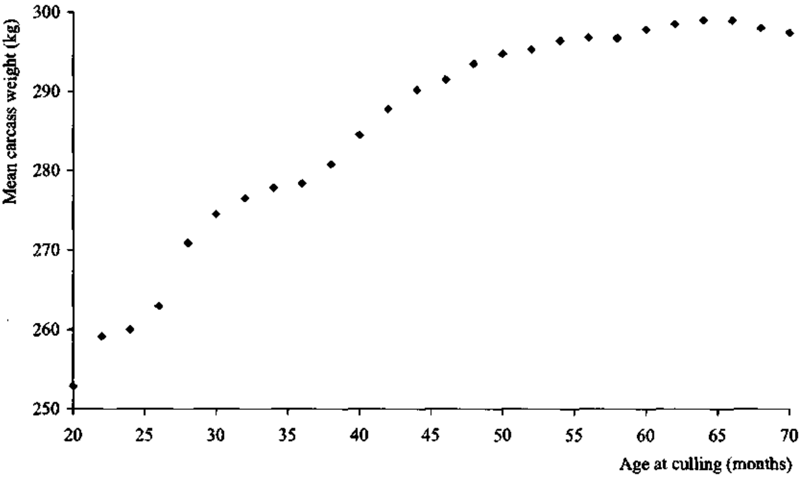

Figure 1. Mean carcass weight of cows with at least 75% Holstein-Friesian genes culled in the period January 1995 through December 1999 (n = 625,948; NRS, unpubl.).

in lower parities when using carcass weights might relate to the higher dressing percentages of younger cows (Van Arendonk, 1985).

The suitability of repeated BW observations at various ages to predict mean BW during life depends on the correlations between repeated observations and on the correlations with mean BW. Therefore, correlations between repeated observations for BW during the first three parities were estimated in Chapter 3. Within each parity, correlations between repeated observations were on average ≥0.84. Correlations between BW observations and mean BW during lactation for BW were also high: increasing from 0.75 in early lactation to ≥0.90 in mid-lactation. Correlations between mean BW in each parity were around 0.80.

These estimates suggest that variation in single BW observations during first lactation highly relates to the variation in mean BW during life and that the use of repeated observations will hardly increase the accuracy of this prediction. The practical implication of these estimates is that data recording for BW can be based on single observations on heifers only.

Breeding value estimation

The suitability of the recorded data for a genetic evaluation relates to the heritability of these data and to the genetic correlations with the breeding goal. For this reason, this study estimated genetic parameters for direct and indirect measurements for BW.

The analysis of field data of lactating heifers (Chapter 4) showed a large genetic variation for BW in the Dutch Holstein-Friesian population. The analyses of the genetic variation across lactation periods (Chapter 5 and 6) showed that genetic correlations between BW observations during lactation were close to unity which means that BW data from all lactation stages can be used to estimate EBVs for mean BW during lactation.

The genetic analyses in this thesis were mainly on lactating heifers and provided therefore not much information on the effects of selection on BW in higher parities. However, the estimate of 0.96 for the genetic correlation between carcass traits of heifers and cows from Liinamo *et al.* (1999) seems to suggest that selection for BW in heifers not only changes BW during first lactation but also in higher parities.

Chapter 4 showed that EBVs for BW can also efficiently be based on conformation scores. For example, the reliability of an EBV for a sire based on 60 daughters with observations for hip height, body depth, muscularity and rump width is 64%. This means that, a genetic evaluation for BW is already possible for most breeding programs even without additional costs for data recording.

The reliability of an EBV for BW within the Dutch breeding scheme might become even higher when also observations on beef traits are considered. For example, young sires have also observations on scored birth weight of 225 calves and carcass weights of 180 veal calves and 10 culled daughters (De Jong, 1997). Despite the relative high numbers of observations for traits on calves, the additional increase in reliability is expected to be minimal due to the low heritabilities and low correlations with mature BW (Groen and Vos, 1995). Although carcass weights of cows are expected to have a high genetic correlation with BW ($r = 0.90$), inclusion of carcass weights of 10 daughters hardly increases the reliability of EBVs for BW.

GENETIC EVALUATION FOR FEED INTAKE AND BODY CONDITION

Feed intake

Until now, a genetic evaluation for DMIC is not included in most breeding programs. However, for two reasons the use of EBVs for DMIC might be attractive when making selection decisions.

The first reason is that direct selection for a higher DMIC can improve the economic efficiency by reducing the relative proportion of concentrates in the diet. Chapter 8 shows that the EV for DMIC increases with higher milk production and more extensive production circumstances. Therefore, it might be speculated that the future relevance of DMIC might increase, when current trends are extrapolated.

The second reason is the relation between DMIC and milk yield. Several authors (e.g. Gravert, 1985; Van Arendonk *et al.*, 1991) reported that with selection for milk yield only, the correlated response in DMIC is not large enough to compensate completely for the additional energy requirements. Results from selection experiments (e.g. Oldenbroek *et al.*, 1997; Buckley *et al.*, 2000) indicate that with selection on milk yield only, the additional energy in early lactation also relies on extra body tissue mobilisation. Direct selection for DMIC might be a tool to reduce the unfavourable effects of the more negative energy balance. Higher DMIC levels might become even more relevant when selection for BW is considered as selection for lower BW on average also results in a lower positive trend for DMIC (Groen and Korver, 1990).

Although heritability estimates suggest significant genetic variation for DMIC, the implementation of a large-scale genetic evaluation for DMIC is problematic.

The first problem is to decide on the optimal moment and frequency of data recording. Chapter 5 estimated genetic parameters for DMIC during first lactation using covariance functions and suggested that DMIC in early and mid lactation are genetically almost uncorrelated. This finding is in line with results of Veerkamp and Thompson (1999) but in contrast with earlier studies. For example, Persuad and Simm (1991) found high genetic correlations (≥0.84) between DMIC observations measured in 6-week periods and Svendsen *et al.* (1994) found high genetic correlations (>0.58) between DMIC observations measured in 5-week periods. The reason for the higher genetic correlations in these studies is not completely clear. One reason might be the longer time period for a DMIC observation. But one might also hypothesise that the phenotypic expression of DMIC in early and later lactation might be different for higher milk production levels compared to lower production levels. The data in Chapter 5 included heifers with a mean and a high milk production level (selection *vs.* control line). Unfortunately, the number of observations was too small to test this hypothesis.

The second problem is that recording of individual feed intake is feasible for small groups of lactating heifers or growing bulls (e.g. Persuad and Simm, 1991; Jakobsen *et al.*, 2000) but unfortunately not for large groups. The use of size traits as an alternative for direct recording is not very attractive as most estimates for genetic correlations between size traits (e.g. capacity, stature and rump width) and DMIC are <0.30 (Veerkamp and Brotherstone, 1997; Parke *et al.*, 1999; Potthast *et al.*, 2000). For example, the reliability of an EBV for DMIC based on 60 daughters is only 9%, assuming genetic correlations between DMIC and body depth, stature, and rump width of 0.30, 0.15 and 0.15, respectively.

Body condition

Selection for BW directly affects the energy balance of lactating cows by changes in maintenance requirements (lower BW) and indirectly by changes in energy intake (lower DMIC) and energy requirements (milk production). Ideally, energy balance is recorded by direct observations for energy balance, but this requires the simultaneous recording of BW, DMIC and milk production which makes a large-scale recording impossible. However BCS, which is often considered as a measure of fat reserves might be a potential indirect measurement of the energy balance.

Until now, most studies on BCS focussed on the phenotypic parameters of BCS and BCS-changes (e.g. Broster and Broster, 1998; Heuer, 2000) rather than on genetic parameters. Therefore, this thesis estimated genetic parameters for BCS during first lactation. In Chapter 5, repeated observations for BCS on heifers were analysed using covariance functions methodology and showed moderate heritabilities (0.21-0.45) and high genetic correlations (0.84-1.00) between repeated observations. In Chapter 7 field data on BCS with only one observation per heifer were analysed. Also for these data, moderate heritabilities (0.30-0.38) and high genetic correlations (>0.86) were found.

This thesis showed that a genetic evaluation for mean BCS can easily be based on data from the conformation scoring system but the high genetic correlations between different lactation months also suggest that a selection for specific patterns of BCS change during lactation is not very effective.

COMBINED SELECTION

For a combined selection strategy, selection decisions can be based on an economic selection index that combines genetic information for the traits of interest. In the Dutch breeding program, animals are ranked on the Durable Performance Sum (DPS) index that combines the EBVs for milk, fat and protein production and durability. The EBVs for milk production traits are based on direct observations, whereas the EBV for durability is based on direct information (culling) and indirect information (conformation scores).

The estimates for the genetic and economic parameters for BW and DMIC from this thesis enable an evaluation of selection strategies that also include EBVs for these traits. This section estimates the effects of combined selection strategies on relative genetic trends and the total economic efficiency. Moreover, the effects of selection on levels for BCS and calving interval (CI) are estimated.

Derivation of selection index

Table 1 presents the genetic standard deviations and EVs for milk production traits, durability, BW, DMIC, BCS and CI. Absolute EVs per genetic s.d. ranged from 6 € (BW) to 75 € (protein). In this study, no EVs are assigned to BCS and CI as they are not yet explicitly included in the present DPS breeding goal.

Table 2 presents the genetic correlations between traits. Most correlations are literature values but some correlations (italic figures in Table 2) were approximated from correlations between sire EBVs using the method of Calo *et al.* (1973). Only EBVs of sires born in the period 1985 through 1995 with a reliability for milk production of at least 90% were included (n = 3325 sires). The EBVs for BW were derived from EBVs for hip height, body depth, rump width and muscularity, whereas EBVs for DMIC were derived from EBVs for hip height, body depth and rump width (NRS, unpubl.). Table 2 shows that BW is positively correlated with milk yield (0.20), DMIC (0.35) and BCS (0.75) but is negatively correlated with CI (–0.42).

Weighting factors (b) for the n single-trait EBVs that maximise the overall economic response of the m breeding goal traits are calculated as $\mathrm{b} = \mathbf{P}^{-1}\mathbf{G}\mathrm{v}$, where b = vector of n weighting factors, $\mathbf{P} = n \times n$ matrix of covariances between EBVs, $\mathbf{G} = n \times m$ matrix of covariances between estimated and true breeding values and v = vector of m discounted EVs (Hazel, 1943).

Table 1. Genetic standard deviations (σ_a) and economic values (EV) for 305-day milk, fat and protein production, durability, body weight, dry-matter intake capacity (DMIC), body condition score (BCS) and calving interval (CI).

	unit	σ_a (units)	EV (€/unit)	$\sigma_a \times \|EV\|$ (€)
Milk	kg	447.0[1]	−0.068[1]	30
Fat	kg	18.9[1]	0.91[1]	17
Protein	kg	13.7[1]	5.45[1]	75
Durability	points	4.5[2]	6.81[2]	31
Body weight	kg	28.7[3]	−0.22[5]	6
DMIC	kg/day	1.0[4]	37[5]	37
BCS		0.86[6]	-	-
CI	days	11.0[7]	-	-

[1] Interbull, 2000.
[2] Vollema *et al.*, 2000.
[3] Chapter 4.
[4] Van Arendonk *et al.*, 1991; Svendsen *et al.*, 1994; Chapter 5.
[5] Chapter 8.
[6] Chapter 7.
[7] Pryce *et al.*, 1997.

Table 2. Genetic correlations between 305-day milk, fat and protein production, durability (DU), body weight (BW), dry-matter intake capacity (DMIC), body condition score (BCS) and calving interval (CI).

	Milk	Fat	Protein	DU	BW	DMIC	BCS	CI
Milk	-	0.55[1]	0.85[1]	0.00	0.20[2]	0.55[3]	−0.30[4]	0.44[5]
Fat		-	0.72[1]	0.00	0.20[2]	0.55[3]	−0.27[4]	0.39[5]
Protein			-	0.00	0.20[2]	0.55[3]	−0.31[4]	0.41[5]
DU				-	*−0.14*	*0.16*	*0.10*	*−0.19*
BW					-	0.35[3]	*0.75*	*−0.42*
DMIC						-	*0.16*	*−0.40*
BCS							-	−0.40[4]
CI								-

[1] Van der Werf and De Boer, 1989.
[2] Ahlborn and Dempfle, 1992; Hietanen and Ojala, 1995; Chapter 6.
[3] Veerkamp, 1998.
[4] Veerkamp *et al.*, 2001.
[5] Hoekstra *et al.*, 1994.

Elements of **P** are based on genetic variances, correlations between estimated and true breeding values and genetic correlations but ignored the phenotypic correlations. In this study it was assumed that EBVs had an accuracy of 100%, which means that matrix **P** includes covariances among true breeding values. Furthermore, when the breeding goal and the index include the same traits weighting factors in the index equal the EVs.

This study did not discount EVs for differences in time and frequency of expression between individual traits because for this set of traits the effect of discounting on the relative weighting was expected to be minimal (Groen, 1989). After one round of selection, the genetic response of the *j*th trait is $b'G_j/\sigma_I \times i$, with G_j is the *j*th column of **G**, σ_I is the standard deviation of the selection index ($= \sqrt{b'Pb}$) and i is the selection intensity. The overall economic response of selection equals $\sigma_I \times i$ €. The selection intensity was arbitrary set to 1 as the focus of this study was more on relative rather than on absolute genetic responses.

To assess the effect of a combined selection strategy on the ranking of breeding candidates the correlation (r) between the present DPS index and each individual alternative index was calculated (James, 1982).

Combined selection for DPS and BW

The estimated selection responses for a breeding goal combining DPS traits and BW are in Table 3. The present DPS index (index I_1) results in positive trends for all breeding goal traits and in an overall economic response of 70.94 €. As correlated effects, the genetic trend in DMIC is positive whereas trends in BCS and CI are unfavourable. As weighting factors of the present DPS index were originally derived for a breeding goal without BW, the economic response might not be maximal. However, when weighting factors are re-estimated for a breeding goal including BW (index I_2), changes in weighting factors and resulting responses were very small. Comparing index I_1 and index I_2 shows that including BW in the breeding goal but not in the selection index has almost no effect on the overall economic response and on the ranking of breeding animals. However, when EBVs for BW are used in the selection index (index I_3), the positive trend in BW decreased largely (–78%) and the genetic trend for milk production decreases slightly (–3%). This index increases the total economic response by 0.4%. However, index I_3 also results in even greater unfavourable trends for BCS and CI and a lower favourable trend for DMIC.

Table 3b shows the effects of using EBVs for BW when assumptions for EVs and genetic correlations are varied. Compared to index I_3, a more negative EV for BW (index I_4) results in a lower positive trend for production and even in a negative trend for BW (–1.9 kg). This index also increases the unfavourable effects on DMIC, BCS and CI. When BW is assumed uncorrelated with milk production (index I_5), the trend in BW becomes even more negative, whereas with a high genetic correlation (index I_6) the genetic trend in BW becomes more positive.

When selection responses of index I_1 were evaluated using the same parameters, economic responses for index I_4, I_5 and I_6 were 70.24, 72.03 and 69.86 €, respectively (results not shown). This means that the additional effect of including EBVs for BW on the overall economic response for these alternatives ranges from 0.4% to 1.6%.

Table 3a. Effect of selection on milk production, durability (DU), body weight (BW), total economic response, dry-matter intake capacity (DMIC), body condition score (BCS) and calving interval (CI).

	I_1	I_2	I_3
Response in breeding goal traits			
Milk (kg)	265	259	258
Fat (kg)	14.3	14.1	14.0
Protein (kg)	11.7	11.6	11.5
DU (points)	1.92	2.00	1.99
BW (kg)	3.2	3.0	0.7
Response (€)	70.94	70.96	71.22
Response in correlated traits			
DMIC (kg/day)	0.539	0.534	0.511
BCS	–0.20	–0.20	–0.27
CI (days)	2.8	2.7	3.2
r	1.000	1.000	0.996

I_1 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU.
I_2 = –0.070 milk + 0.86 fat + 5.45 protein + 7.00 DU.
I_3 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW.

Table 3b. Effect of selection on milk production, durability (DU), body weight (BW), total economic response, dry-matter intake capacity (DMIC), body condition score (BCS) and calving interval (CI).

	I_4	I_5	I_6
Response in breeding goal traits			
Milk (kg)	250	262	254
Fat (kg)	13.7	14.2	13.9
Protein (kg)	11.2	11.6	11.4
DU (points)	2.04	1.96	2.02
BW (kg)	–1.9	–4.2	5.7
Response (€)	71.35	72.30	70.13
Response in correlated traits			
DMIC (kg/day)	0.479	0.504	0.519
BCS	–0.33	–0.26	–0.27
CI (days)	3.6	3.2	3.3
r	0.984	0.996	0.996

I_4 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.44 BW; EV(BW) = –0.44 €.
I_5 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW; r_g(BW, MY) = 0.00.
I_6 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW; r_g(BW, MY) = 0.40.

Combined selection for DPS, BW and DMIC

The estimated selection responses for a breeding goal combining DPS traits, BW and DMIC are in Table 4.

The total economic response of the present DPS index (index I_7) increases by about 20 € (+28%) only by accounting for the economic effects of the positive trend in DMIC (Table 4a). When weighting factors for DPS traits were optimised for a breeding goal with DMIC (index I_8), positive trends for milk production, BW and DMIC increase but the positive trend for durability decreases. As correlated effects, trends in BCS and CI become more unfavourable.

For a selection index with a EBV for BW but not for DMIC (index I_9) the weighting for BW becomes positive. Most likely, this is due to the positive correlation between BW and DMIC and the relative high EV for DMIC. Selection responses are comparable to index I_8, except for the higher positive trends in BW and DMIC.

An index with EBVs for both BW and DMIC (index I_{10}), increases genetic trends in milk production (+9%), BW (+38%) and DMIC (+42%). The total economic response increases to 95.59 € (+5%). Compared to the present DPS index, index I_{10} largely reduces the unfavourable trends in BCS (–31%) and CI (–75%). This index might also result in a clear reranking of breeding animals ($r = 0.951$) when compared to the present index.

Table 4b shows the effects of using EBVs for DMIC when EVs, genetic correlations and reliabilities are varied. With a lower EV for DMIC (index I_{11}), positive trends for milk production, BW and DMIC increase less. A lower genetic correlation between DMIC and MY reduces the economic response (index I_{12}), whereas the economic response increased for a lower correlation between DMIC and BW (index I_{13}). Index I_{14} uses EBVs for DMIC with a reliability of only 9%, based on conformation traits of 60 daughters. For this situation, the effect of including EBVs for DMIC is limited.

Practical implementation

The economic response of a dairy cattle breeding scheme is maximal when full information on all traits of interest is considered. Until now, most breeding organisations do not yet consider BW and DMIC when making selection decisions. Breeding organisations that do not have direct information on BW or DMIC but do record conformation data can consider at least three options for a combined selection strategy without additional costs for data recording.

These options are illustrated here for the Dutch breeding program.

The first option adds BW to the breeding goal and adds EBVs for BW in the selection index (= index I_3). Compared to the present selection strategy

Table 4a. Effect of selection on milk production, durability (DU), body weight (BW), dry-matter intake capacity (DMIC), total economic response, body condition score (BCS) and calving interval (CI).

	I_7	I_8	I_9	I_{10}
Response in breeding goal traits				
Milk (kg)	265	300	300	288
Fat (kg)	14.3	15.1	15.1	14.5
Protein (kg)	11.7	12.0	12.0	11.5
DU (points)	1.92	1.84	1.84	1.76
BW (kg)	3.2	3.7	4.6	4.4
DMIC (kg/day)	0.539	0.581	0.588	0.768
Response (€)	90.89	91.70	91.74	95.59
Response in correlated traits				
BCS	–0.20	–0.22	–0.20	–0.14
CI (days)	2.8	3.2	3.1	0.7
r	1.000	0.991	0.991	0.951

I_7 = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU.
I_8 = –0.039 milk + 1.58 fat + 5.35 protein + 8.32 DU.
I_9 = –0.039 milk + 1.56 fat + 5.35 protein + 8.41 DU + 0.10 BW.
I_{10} = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW + 37 DMIC.

Table 4b. Effect of selection on milk production, durability (DU), body weight (BW), dry-matter intake capacity (DMIC), total economic response, body condition score (BCS) and calving interval (CI).

	I_{11}	I_{12}	I_{13}	I_{14}
Response in breeding goal traits				
Milk (kg)	279	267	289	299
Fat (kg)	14.5	13.7	14.6	15.1
Protein (kg)	11.7	11.0	11.6	11.9
DU (points)	1.89	1.86	1.8	1.83
BW (kg)	2.8	4.6	6.6	4.6
DMIC (kg/day)	0.665	0.674	0.759	0.597
Response (€)	82.23	90.71	95.10	91.93
Response in correlated traits				
BCS	–0.20	–0.15	–0.14	–0.20
CI (days)	1.8	0.7	0.7	2.9
r	0.951	0.932	0.956	0.989

I_{11} = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW + 19 DMIC; EV (DMIC) = 19 €.
I_{12} = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW + 37 DMIC; r_g (DMIC, MY) = 0.35.
I_{13} = –0.068 milk + 0.91 fat + 5.45 protein + 6.81 DU – 0.22 BW + 37 DMIC. r_g (DMIC, BW) = 0.55.
I_{14} = –0.041 milk + 1.53 fat + 5.36 protein + 8.33 DU + 0.08 BW + 20 DMIC. r_{ih}^2 (DMIC) = 0.09.

(= index I_1), this results in smaller positive trends in BW, DMIC, durability and milk production and greater unfavourable genetic trends in BCS and CI.

An advantage of this index is the easy interpretation of the selection index which is a simple weighting of EBVs by their EVs. A disadvantage of this index is that it has unfavourable effects on the genetic trends for DMIC, BCS and CI. When accounting for the lower response in DMIC, the total economic response of this index is 90.13 € (= 71.22 € + 0.511 × 37 €) which is slightly less than for the current DPS index (= 70.94 € + 0.539 × 37 €).

The second option adds both BW and DMIC to the breeding goal but adds only EBVs for BW to the index (= index I_9). This results in a higher trend for milk production but also in a lower positive trend for durability and a greater unfavourable trend for CI. With this option, the estimated economic response of selection is higher than in the first option. However, the positive weighting of the EBV for BW in this index might cause confusion to practical breeders as EBVs for BW are now used to increase DMIC (positive EV) rather than to decrease BW (negative EV). Another disadvantage is that, compared to the present DPS index, this index results in higher trends in production but also in more unfavourable trends for durability and CI which might be undesirable from a welfare point of view.

The third option adds both BW and DMIC to the breeding goal and adds EBVs for both traits to the index (= index I_{14}). For this option, genetic trends and the total economic response change only marginally compared to the second option which relates to the very low reliability of EBVs for DMIC.

The discussed options illustrate that determining the optimal weighting within a combined selection strategy is not easy as it largely depends on the methods of accounting for (correlated) selection responses. When the effects of correlated changes in DMIC and CI are not considered, a negative weighting of BW might have a small positive effect on the total economic response (Index I_3). However, when the effects of a negative weighting of BW on DMIC are included, the same index (without EBVs for DMIC) will even reduce the economic response. Furthermore, the discussed options in this thesis only marginally considered the effects of a negative weighting of BW on health and fertility. Unfortunately, estimates for the genetic relations between BW and health and fertility are still scarce. However, recent studies (e.g. Pryce *et al.*, 2000; Wassmuth *et al.*, 2000) suggest favourable genetic relations between a high DMIC and BCS at the one side and health and fertility traits at the other side. Considering the positive correlations between BW and DMIC and BCS this would imply that a negative weighting on BW would become less attractive.

MAIN CONCLUSIONS

From this thesis the following conclusions can be made:

1. Lactating dairy cows have a large phenotypic variation for BW. This variation is highly repeatable, both within and across the first three lactations (Chapter 3).

2. Heritability estimates for BW indicated that mean BW levels can efficiently be changed by genetic selection using single observations (Chapter 4). However, it is difficult to change BW-change patterns during lactation (Chapter 5 and 6).

3. When a large-scale genetic evaluation for BW is considered, the use of routinely scored conformation traits is an attractive alternative for weighing animals (Chapter 4).

4. The DMIC of lactating heifers has a moderate heritability, but the low genetic correlations between DMIC observations in early and mid lactation complicate decisions on selection strategies for DMIC. Additional studies on the dynamics of the genetic variation during lactation are required (Chapter 5).

5. Genetic correlations between BW and milk production traits are small (<0.20); size traits such as hip height and body depth have a somewhat higher correlation with milk production traits (0.20-0.30) (Chapter 6).

6. The BCS of lactating heifers has a moderate heritability (0.30-0.40). The high genetic correlations between BCS observations in different lactation months indicate that selection for mean BCS during lactation is possible but not for BCS changes (Chapter 5 and 7).

7. Under Dutch production circumstances, the EV for BW is negative whereas the EV for DMIC is positive. Extrapolation of current trends might suggest that the economic relevance of both traits increase in future.

8. Adding EBVs for BW and DMIC to the present selection strategy increases the positive trends in BW, milk production and DMIC and reduces the unfavourable trends in BCS and CI. The additional total economic response

highly depends on the EV of DMIC and the reliability of the EBV for DMIC.

9. Although weighting in the breeding goal for BW is negative, a negative index weighting of EBVs for BW cannot be recommended for present Dutch production circumstances.

REFERENCES

Ahlborn, G. and L. Dempfle, 1992. Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livest. Prod. Sci.* 31: 205-219.

Broster, W.H. and V.J. Broster, 1998. Body score of dairy cows: review. *J. Dairy Res.* 65: 155-173.

Buckley, F., Dillon, P., Crosse, S., Flynn, F. and M. Rath, 2000. The performance of Holstein Friesian dairy cows of high and medium genetic merit for milk production on grass-based feeding systems. *Livest. Prod. Sci.* 64: 107-119.

Calo, L.L., McDowell, R.E., Van Vleck, L.D. and P.D. Miller, 1973. Genetic aspects of beef production among Holstein-Friesian pedigrees selected for milk production. *J. Anim. Sci.* 37: 676-682.

De Jong, G., 1997. *Genetische parameters voor slachtkenmerken bij melkkoeien, blanke kalveren, rosé kalveren en vleesstieren.* Nederlands Rundvee Syndicaat. Arnhem, The Netherlands. 21 pp.

Gravert, H.O., 1985. Genetic factors controlling feed efficiency in dairy cows. *Livest. Prod. Sci.* 13: 87-99.

Groen, A.F., 1988. Derivation of economic values in cattle breeding. A model at farm level. *Agric. Syst.* 27: 195-213.

Groen, A.F., 1989. *Cattle breeding goals and production circumstances.* Ph.D. Thesis. Wageningen Agricultural University. Wageningen, The Netherlands. 167 pp.

Groen, A.F. and S. Korver, 1990. Feed intake capacity of lactating cows in dairy and dual purpose cattle selection. *J. Anim. Breed. Genet.* 107: 389-396.

Groen, A.F. and H. Vos, 1995. Genetic parameters for body weight and growth in Dutch Black-and-White replacement stock. *Livest. Prod. Sci.* 41: 201-206.

Hazel, L.N. 1943. The genetic basis for constructing selection indexes. *Genetics* 28: 476-490.

Heuer, C., 2000. *Negative energy balance in dairy cows - prediction, consequences and prevention.* Ph.D. Thesis. Utrecht University. Utrecht, The Netherlands. 212 pp.

Hietanen, H. and M. Ojala, 1995. Factors affecting body weight and its association with milk production traits in Finnish Ayrshire and Friesian cows. *Acta Agric. Scand., Sect. A, Anim. Sci.* 45: 17-25.

Hoekstra, J., Van der Lugt, A.W., Van der Werf, J.H.J. and W. Ouweltjes, 1994. Genetic and phenotypic parameters for milk production and fertility traits in upgraded dairy cattle. *Livest. Prod. Sci.* 40: 225-232.

INTERBULL, 2000. *National genetic evaluation programmes for dairy production traits practised in INTERBULL member countries 1999-2000.* INTERBULL bulletin no. 24. Intern. Bull Evaluations Service. Uppsala, Sweden. 111 pp.

Jakobsen, J.H., Madsen, P., Jensen, J., Petersen, P.H. and G. Aa. Pedersen, 2000. Genetic correlations between beef traits measured on young performance test bulls and daughter milk yield. *Acta Agric. Scand., Sect. A, Anim. Sci.* 50: 39-46.

James, J.W., 1982. Construction, uses and problems of multitrait selection indices. *Proc. 2nd World Congr. Genet. Appl. Livest. Prod.* 5: 130-139.

Liinamo, A.-E., Ojala, M. and J.A.M. Van Arendonk, 1999. Relationships of body weight and carcass quality traits with first lactation milk production in Finnish Ayrshire cows. *Livest. Prod. Sci.* 60: 271-279.

Oldenbroek, J.K., Galesloot, P.A.J., Pool, M.H. and J.H.J. Van der Werf, 1997. *Effects of selection for milk yield on feed intake and metabolism of heifers in early lactation.* Paper presented at EAAP-meeting. Vienna, Austria.

Parke, P., Kennedy, B.W., Dekkers, J.C.M., Moore, R.K. and L. Jairath, 1999. Genetic and phenotypic parameter estimates between production, feed intake, feed efficiency, body weight and linear type traits in first lactation Holsteins. *Can. J. Anim. Sci.* 79: 425-431.

Persuad, P. and G. Simm, 1991. Genetic and phenotypic parameters for yield, food intake and efficiency of dairy cows fed *ad libitum*. 2. Estimates for part lactation measures and their relationship with 'total' lactation measures. *Anim. Prod.* 52: 445-450.

Potthast, J., Tholen, E. and W. Trappmann, 2000. Untersuchungen zur Integration des Merkmals Futteraufnahmekapazität wachsender Bullen in Besamungszuchtprogramme bei Milchrindern. 1. Mitteilung: Schätzung von genetischen Parametern. *Züchtungsk.* 72: 88-101.

Pryce, J.E., Coffey, M.P. and S. Brotherstone, 2000. The genetic relationship between calving interval, body condition score and linear type and management traits in registered Holsteins. *J. Dairy Sci.* 83: 2664-2671.

Pryce, J.E., Veerkamp, R.F., Thompson, R., Hill, W.G. and G. Simm, 1997. Genetic aspects of common health disorders and measures of fertility in Holstein Friesian dairy cattle. *Anim. Sci.* 65: 353-360.

Svendsen, M., Skipeness, P. and Mao, I.L., 1994. Genetic correlations in the feed conversion complex of primiparous cows at a recommended and reduced plane of nutrition. *J. Anim. Sci.* 72: 1441-1449.

Van Arendonk, J.A.M., 1985. A model to estimate the performance, revenues and costs of dairy cows under different production and price situations. *Agric. Syst.* 16: 157-189.

Van Arendonk, J.A.M., Nieuwhof, G.J., Vos, H. and S. Korver, 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. *Livest. Prod. Sci.* 29: 263-275.

Van der Werf, J.H.J. and W. De Boer, 1989. Estimation of genetic parameters in a crossbred population of Black and White dairy cattle. *J. Dairy Sci.* 72: 2615-2623.

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. and S. Brotherstone, 1997. Genetic correlations between linear type traits, feed intake, live weight and condition score in Holstein Friesian dairy cattle. *Anim. Sci.* 64: 385-392.

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

Veerkamp, R.F., Koenen, E.P.C. and G. De Jong, 2001. Genetic correlations between body condition scores, yield and fertility in Holstein heifers estimated by random regression models. *J. Dairy Sci.*: submitted.

Vollema, A.R., Van der Beek, S., Harbers, A.G.F. and G. De Jong, 2000. Genetic evaluation for longevity of Dutch dairy bulls. *J. Dairy Sci.* 83: 2629-2639.

Wassmuth, R., Boelling, D., Madsen, P., Jensen, J. and B. Bech Andersen, 2000. Genetic parameters of disease incidence, fertility and milk yield of first parity cows and the relation to feed intake of growing bulls. *Acta Agric. Scand., Sect. A, Anim. Sci.* 50: 93-102.

SUMMARY

This thesis deals with selection for body weight (BW) in dairy cattle. The economic efficiency of present breeding schemes might increase further when selection decisions consider information on BW as BW relates to feed costs and revenues from beef production. However, the practical implementation of such a selection strategy is hindered by limited knowledge on procedures for data recording and genetic evaluation. Furthermore, the economic relevance of selection for BW is not clear. Therefore, the aim of this thesis was to study the possibilities and economic relevance of selection strategies for BW in dairy cattle.

Data recording and genetic evaluation

To obtain information on the optimal moment and frequency of data recording, this thesis analysed repeated BW observations on growing and lactating heifers from experimental herds.

Chapter 2 studied growth patterns of 743 heifers from birth until first calving by fitting two mathematical functions. The Von Bertalanffy function fitted the data better than did the two-phase logistic growth function. Mature BW was predicted by extrapolation. The results suggested that BW at first calving has a high correlation with mature BW, indicating that BW at first calving is a good predictor of mature BW.

Chapter 3 analysed weekly means for BW during 452 lactations (239 cows) to estimate non-genetic effects and repeatabilities during the first three parities. The most important non-genetic effects on BW were feeding, lactation stage, pregnancy stage and age at calving. On average, BW increased from 537 kg after first calving until 633 kg after third calving. Average maximum BW loss ranged from 22 to 26 kg and was obtained around week 10 of lactation, but individual variation was large. Observations for BW were highly repeatable within and across parities. Observations at any lactation stage were highly correlated with mean BW during lactation. These results indicated that a single BW observation on a lactating heifer is a good predictor of mean BW during the first three parities.

In Chapter 4, the genetic variation for BW was estimated using field data on 7344 lactating heifers from 560 Dutch herds. Mean unadjusted mean BW was 546 ± 57 kg. After adjusting for non-genetic effects (lactation stage, pregnancy stage, parity of dam, herd and age at calving) a genetic standard deviation of 29 kg and a heritability of 0.33 were found. Chapter 4 also studied the suitability of heart girth, hip height and linear conformation scores as indirect measurements for BW. Observations for BW had high genetic correlations with heart girth (0.77), hip

height (0.50), body depth (0.48), rump width (0.43) and muscularity (0.58). These correlations showed that a large-scale genetic evaluation for BW can easily be based on conformation data that are already routinely recorded in most breeding schemes.

Chapter 5 and 6 studied the dynamic aspects of BW during lactation and found that genetic correlations for BW observations in different lactation months were close to unity. These results indicated that it is possible to select for mean BW during lactation but that opportunities to select for specific BW change patterns were limited.

Genetic evaluation for feed intake and body condition score

As selection for BW also affects dry-matter intake capacity (DMIC) and body condition score (BCS), this thesis also studied the genetic aspects for DMIC and BCS. Special interest in this study was on the dynamic aspects of the genetic variation during lactation. In Chapter 5 the genetic parameters of BW and DMI during lactation were estimated from repeated observations from experimental data on 469 heifers. These observations were analysed using covariance functions that describe the genetic background of BCS and DMIC as a continuous function of lactation stage. Heritability estimates for BCS and DMIC during lactation were in the range 0.21-0.45 and 0.18-0.37, respectively. The high genetic correlations between repeated BCS observations suggested that the genetic background of BCS is constant during lactation. However, the low correlations between DMIC observations in early and mid-lactation suggested that the genetic background for DMIC was not constant during lactation.

Genetic parameters for BCS were also estimated from routinely collected BCS data including 135,017 lactating heifers from 9701 herds (Chapter 7). On a 1 to 9 scale, mean BCS was 4.5 and 4.9 for Black-and-White and Red-and-White dairy heifers, respectively. Heritability estimates for both breeds were 0.38 and 0.30, respectively. As in Chapter 5, estimates for the genetic correlations between different lactation months were high. These results showed that breeding values for BCS can easily be estimated from field data. These results also implied that estimated breeding values (EBVs) can be used to change mean BCS levels by selection but that it is difficult to select for systematic BCS-changes during lactation.

Combined selection

For optimising a combined selection strategy, estimates for the genetic correlations among traits and for the effect of genetic improvement on the economic efficiency (economic values) are needed.

Chapter 6 estimated the genetic correlations between BW and 305-day milk production of heifers. Genetic correlations between BW and 305-day production for milk, fat and protein were low (–0.14 to 0.26). This analysis did not confirm results from earlier studies that indicated that the correlation between size and yield depended on the lactation stage.

In Chapter 8 the effect of changes in BW and DMIC on the economic efficiency was studied. A farm model was used to estimate economic values (EVs) for BW and DMIC. As production circumstances at the moment of expression can differ largely from present production circumstances, Chapter 8 also evaluated three scenarios for changes in production circumstances until 2008. The present EV for BW was negative and might become more negative under future production circumstances with lower beef prices and higher milk production levels. The present EV for DMIC was positive and might become more positive under more extensive production circumstances with higher milk production levels.

Finally, Chapter 9 illustrated the effects of selection for BW on the genetic trends and economic efficiency for the Dutch breeding program. Starting from the present selection index including milk production and durability, several alternative selection strategies were evaluated. Including EBVs for BW without accounting for changes in DMIC reduced the positive trends in BW (–78%), milk production (–3%) and DMIC (–5%) but increased the unfavourable trends in BCS (–32%) and calving interval (+16%). The additional economic response of this alternative was small (+0.4%). When accounting for changes in DMIC, the optimal weighting for EBVs for BW in the index became positive. In this situation, genetic trends for milk production, BW and DMIC increased. The economic response increased by 0.9%. However, the main disadvantage of this alternative is the unfavourable effect on durability and calving interval. An index with known EBVs for both BW and DMIC resulted in higher trends for milk production, BW and DMIC and favourable trends for BCS and calving interval. Despite the negative weighting on BW in the index, the positive genetic trend for BW was even higher than in the present selection strategy. The net effect on the economic response of that index was relatively high (+5%). The responses of this index were highly sensitive to the EV and the reliability of EBVs for DMIC.

Main conclusions

Lactating dairy cows have a large phenotypic variation for BW, which is highly repeatable, both within and across lactations. The moderate heritabilities for BW indicate that genetic selection can efficiently change mean BW levels. For a large-scale genetic evaluation for BW, size traits from the regular conformation scoring system can be used as an attractive alternative for weighing animals.

The moderate heritabilities for DMIC of lactating heifers suggest that also DMIC can be changed by genetic selection but the low genetic correlations between DMIC observations in early and mid lactation largely complicate selection strategies for DMIC.

Genetic correlations between BW and milk production traits are small (<0.20), whereas correlations between size traits such as hip height and body depth and milk production are somewhat higher (0.20-0.30).

The BCS of lactating heifers has a moderate heritability (0.30-0.40) which enables a genetic evaluation for BCS.

Under Dutch production circumstances, EVs were negative for BW and positive for DMIC. The inclusion of EBVs for BW and DMIC in the present selection strategy has seems to be attractive but is hard to implement under practical conditions as no reliable EBVs for DMIC can be obtained. It was concluded that despite a negative weighting of BW in the breeding goal, a negative weighting of EBVs for BW cannot be recommended under present Dutch production circumstances.

SAMENVATTING

Dit proefschrift gaat over selectie op lichaamsgewicht (LG) in melkvee. De economische efficiëntie van de huidige fokprogramma's kan mogelijk verhoogd worden door bij selectiebeslissingen ook rekening te houden met LG omdat LG samenhangt met voerkosten en opbrengsten uit omzet en aanwas. Echter, de implementatie van een gecombineerde selectiestrategie is moeilijk door de beperkte kennis over procedures voor dataverzameling en de genetische evaluatie voor LG. Bovendien is het economische belang van het gebruik van informatie over LG niet duidelijk. Het doel van dit proefschrift is dan ook om de mogelijkheden en economische relevantie te onderzoeken van een gecombineerde selectie-strategie voor melkvee.

Data verzameling en genetische evaluatie

Om informatie te krijgen over het optimale moment en de optimale frequentie van gegevensverzameling werden in dit proefschrift herhaalde waarnemingen voor LG van groeiende en lacterende dieren geanalyseerd.

In Hoofdstuk 2 werden groeipatronen van 743 vaarzen van geboorte tot de eerste keer afkalven met twee wiskundige functies beschreven. De Von Bertalanffy functie beschreef de data beter dan de twee-fasen logistische functie. Volwassen LG werd bepaald via extrapolatie. De resultaten suggereren dat LG bij de eerste keer afkalven sterk samenhangt met het volwassen LG en dat LG bij de eerste keer afkalven daarom een goede voorspeller van het volwassen LG is.

In Hoofdstuk 3 werden niet-genetische effecten en herhaalbaarheden voor LG gedurende de eerste drie pariteiten geschat op basis van weekgemiddelden van 239 koeien gedurende 452 lactaties. De belangrijkste niet-genetische effecten waren voeding, lactatiestadium, drachtigheidsstadium en leeftijd bij afkalven. Gemiddeld nam het LG toe van 537 kg na de eerste keer afkalven tot 633 kg na de derde keer afkalven. Het gemiddelde maximale LG verlies varieerde van 22 tot 26 kg en trad op rond week 10, maar de individuele variatie was groot. De herhaalbaarheid voor LG was groot zowel binnen als over lactaties. Observaties waren op ieder lactatiemoment hoog gecorreleerd met het gemiddelde LG tijdens de lactatie. Deze resultaten suggereerden dat een enkele waarneming voor LG tijdens de lactatie een goede voorspeller is voor het gemiddelde LG tijdens de eerste drie lactaties.

In Hoofdstuk 4 werd de genetische variatie voor LG geschat op basis van velddata van 7344 lacterende vaarzen van 560 bedrijven. Het ongecorrigeerde gemiddelde LG was 546 ± 57 kg. Na correctie voor niet-genetische effecten (lactatiestadium, drachtigheidsstadium, pariteit van de moeder, bedrijf en leeftijd bij afkalven) werd

een genetische spreiding van 29 kg en een erfelijkheidsgraad van 0,33 gevonden.
In Hoofdstuk 4 werd ook gekeken naar de bruikbaarheid van borstomvang, kruishoogte en lineaire exterieurscores als voorspellers voor LG. Waarnemingen voor LG waren genetisch hoog gecorreleerd met borstomvang (0,77), kruishoogte (0,50), inhoud (0,48), kruisbreedte (0,43) en bespiering (0,58). Deze correlaties lieten zien dat een grootschalige genetische evaluatie voor LG gemakkelijk gebaseerd kan worden op kenmerken die in de meeste fokprogramma's al worden vastgelegd.
De dynamische aspecten van LG werden bekeken in Hoofdstuk 5 en 6. Gevonden werd dat de genetische correlaties voor LG waarnemingen in de verschillende lactatiemaanden bijna gelijk aan 1 waren. Deze resultaten geven aan dat het gemakkelijk is om het gemiddelde LG tijdens de lactatie via fokkerij te veranderen, maar dat het erg moeilijk is om te selecteren op specifieke gewichtspatronen tijdens de lactatie.

Genetische evaluatie van voeropname en conditiescore
Omdat selectie op LG ook de voeropnamecapaciteit (VOC) en de conditiescore (CS) beïnvloedt zijn in dit proefschrift ook de genetische aspecten van VOC en CS bestudeerd. Speciale aandacht werd besteed aan de dynamische aspecten van de genetische variatie tijdens de lactatie. In Hoofdstuk 5 werden de genetische parameters voor LG en VOC tijdens de lactatie geschat op basis van herhaalde waarnemingen van 469 vaarzen. Deze waarnemingen werden geanalyseerd met covariantiefuncties die de genetische variatie voor de kenmerken beschreven als een functie van het lactatiestadium.
Geschatte erfelijkheidsgraden voor CS and VOC tijdens de lactatie varieerden van 0,21 tot 0,45 en van 0,18 tot 0,37, respectievelijk. De hoge genetische correlaties tussen herhaalde waarnemingen voor CS geven aan dat de genetische achtergrond van CS constant is tijdens de lactatie. Echter, bij VOC suggereren de lage correlaties tussen waarnemingen in het begin en het midden van de lactatie dat de genetische achtergrond voor VOC afhangt van het lactatiestadium.
Genetische parameters voor CS werden ook geschat op basis van routinematig verzamelde data van 135.017 lacterende vaarzen op 9701 bedrijven (Hoofdstuk 7). Op de gebruikte 1-9 schaal was de gemiddelde CS 4,5 en 4,9 voor zwart- en roodbont, respectievelijk. Erfelijkheidsgraden voor zwart- en roodbont waren 0,38 en 0,30, respectievelijk. Net als in Hoofdstuk 5 waren de genetische correlaties tussen CS op verschillende lactatiestadia hoog. Deze resultaten laten zien dat fokwaarden voor CS geschat kunnen worden op basis van velddata. De resultaten suggereren dat de gemiddelde CS tijdens de lactatie door selectie gemakkelijk

veranderd kan worden, maar dat het moeilijk is om te selecteren op specifieke CS veranderingen tijdens de lactatie.

Gecombineerde selectie

Voor een optimale gecombineerde selectie-strategie zijn schattingen nodig voor de genetische correlaties tussen kenmerken en voor het effect van genetische veranderingen op de economische efficiëntie (economische waarden).
In Hoofdstuk 6 worden de genetische correlaties geschat tussen LG en 305-dagen melkproductie van vaarzen. De genetische correlaties tussen LG en 305-dagen productie van melk, vet en eiwit waren laag (–0,14 tot 0,26). Deze resultaten bevestigen niet eerdere resultaten die suggereerden dat de correlatie tussen LG en melkproductie afhangt van het lactatiestadium.
In Hoofdstuk 8 werd het effect van veranderingen in LG en VOC op de economische efficiëntie geschat. Een bedrijfsmodel werd gebruikt om de economische waarden (EW) te van LG en VOC te schatten. Omdat de productie-omstandigheden op het moment van expressie sterk kunnen afwijken van de huidige productieomstandigheden zijn in dit hoofdstuk drie scenario's voor de ontwikkelingen in productieomstandigheden tot 2008 doorgerekend. De huidige EW voor LG is negatief en wordt sterker negatief bij productieomstandigheden met lagere vleesprijzen en hogere melkproductieniveaus. De huidige EW voor VOC is positief en kan sterker positief worden onder extensievere productie-omstandigheden en hogere melkproductieniveaus.
Tot slot worden in Hoofdstuk 9 de effecten van selectie op de genetische trends en de economische efficiëntie voor het Nederlandse fokprogramma geïllustreerd. Met de huidige selectie-index (melkproductie en duurzaamheid) als uitgangspunt werden alternatieve selectie-strategieën bekeken. Het gebruik van fokwaarden voor LG zonder rekening te houden met veranderingen in VOC reduceerde de positieve trends in LG (–78%), melkproductie (–3%) en VOC (–5%) maar vergrootte ook de ongunstige trends voor CS (–32%) en tussenkalftijd (+16%). De extra economische respons van dit alternatief is beperkt (+0,4%). Als rekening wordt gehouden met gecorreleerde effecten in VOC dan was de optimale weging van de fokwaarde voor LG in de index positief. In dat geval namen de genetische trends voor melkproductie, LG en VOC toe. De economische respons nam toe met 0,9%. Echter, het grootste nadeel van dit alternatief is het ongunstige effect op duurzaamheid en tussenkalftijd. Een index met bekende fokwaarden voor zowel LG als VOC resulteerde in hogere trends voor melkproductie, LG en VOC en gunstige trends voor CS en tussenkalftijd. Ondanks de negatieve inweging van LG in de index, was de positieve genetische trend voor LG zelfs hoger dan in de

huidige selectie-strategie. Het netto effect op de economische respons was relatief hoog (+5%). De respons van deze index was sterk afhankelijk van de EW en van de betrouwbaarheid van de fokwaarde voor VOC.

Conclusies

De fenotypische variatie in LG voor lacterende koeien is groot en heeft een hoge herhaalbaarheid zowel binnen als over lactaties. De gevonden erfelijkheidsgraden voor LG laten zien dat het gemiddelde LG via selectie gemakkelijk te veranderen is. Voor een grootschalige genetische evaluatie voor LG is het gebruik van exterieurgegevens een aantrekkelijk alternatief voor het wegen van dieren.

De geschatte erfelijkheidsgraden voor VOC bij lacterende vaarzen suggereren dat ook VOC via genetische selectie veranderd kan worden, maar deze selectie wordt wel bemoeilijkt door de lage genetische correlaties tussen VOC in het begin en het midden van de lactatie.

De genetische correlaties tussen LG en melkproductie zijn laag (<0,20); exterieurkenmerken zoals kruishoogte en inhoud hebben een iets hogere correlatie (0,20-0,30).

De erfelijkheidsgraad van CS bij lacterende vaarzen bedraagt 0,30-0,40 en biedt hiermee mogelijkheden voor selectie.

Onder Nederlandse omstandigheden is de EW voor LG negatief terwijl dit voor VOC positief is.

Het gebruik van fokwaarden voor LG en VOC bij de huidige selectie-index lijkt aantrekkelijk maar is moeilijk uit te voeren omdat geen betrouwbare fokwaarden voor VOC beschikbaar zijn. Geconcludeerd werd dat, ondanks de negatieve EW voor LG in het fokdoel, een negatieve inweging van fokwaarden voor LG niet aanbevolen kan worden voor de huidige Nederlandse productieomstandigheden.

NAWOORD

Bij het tot stand komen van dit proefschrift zijn diverse personen betrokken geweest. Enkele van hen wil ik hier in het bijzonder noemen.
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Erwin

CURRICULUM VITAE

Erwin Petrus Carolus Koenen werd geboren op 27 juli 1971 te Nijmegen. Hij groeide op in Heijen (L.) en behaalde in 1989 het VWO-diploma aan het Elzendaal College te Boxmeer. In dat jaar begon hij met de studie Zoötechniek aan de toenmalige Landbouwuniversiteit te Wageningen. De stage werd in 1992 uitgevoerd aan de Sveriges Lantbruksuniversitet te Uppsala. In augustus 1994 behaalde hij met lof het doctoraalexamen Zoötechniek met als afstudeervakken Veefokkerij en Gezondheidsleer en Reproductie. Van juli tot en met december 1994 werkte hij voor het Koninklijk Warmbloed Paardenstamboek Nederland. In januari 1995 werd hij aangesteld als Assistent-In-Opleiding bij de toenmalige Vakgroep Veefokkerij van de Landbouwuniversiteit, alwaar het in dit proefschrift beschreven onderzoek is uitgevoerd. Een deel van dit onderzoek werd uitgevoerd bij het Scottish Agricultural College te Edinburgh. Sinds april 1999 werkt hij bij de afdeling R&D van de Koninklijke Coöperatie Rundveeverbetering Delta u.a. te Arnhem.