Selection Responses for Clinical Mastitis and Protein Yield in Two Norwegian Dairy Cattle Selection Experiments

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ABSTRACT

Inferences from two dairy cattle selection experiments, in which sires were selected from external sources, were drawn by using an animal model to analyze data from the entire population. The first selection experiment was carried out in the period from 1978 to 1989 and included groups selected for high milk production (HMP) and low milk production (LMP). Each year, the highest ranking proven sires for milk production, from the most recent group of Norwegian Dairy Cattle (NRF) test bulls, were selected and mated to the cows in the HMP group. A group of sires with low milk production indices from progeny testing in 1978 and 1979 were used as sires in the LMP group during the entire experiment. The second selection experiment, which started in 1989, included one high protein yield (HPY) group and one low clinical mastitis (LCM) group. The highest ranking proven NRF sires for protein yield and mastitis resistance were selected each year from the most recent group of progeny tested bulls and used as sires in the HPY and LCM groups, respectively. Genetic trends for protein yield were positive (as expected) for HMP and HPY cows, and negative for LMP and LCM cows. Estimates of annual genetic trends for clinical mastitis were +0.23, -0.02, +0.04, and -0.91% per year for HMP, LMP, HPY, and LCM cows, respectively. The difference in genetic trend of clinical mastitis between HMP and HPY groups, both selected for increased milk production, reflects the gradual change in the NRF breeding objective towards more weight on health relative to milk over the last 20 yr. After four cow generations, the genetic difference in mastitis between HMP and LMP group cows was 3.1% clinical mastitis, a correlated response to selection for increased milk production. The genetic difference between LCM and HPY cows of 8.6% clinical mastitis

after three cow generations is mainly a result of direct selection against clinical mastitis in the LCM group. In the NRF population, an approximately flat genetic trend for clinical mastitis was found for cows born from 1976 to 1990, whereas cows born after 1990 showed a genetic improvement equivalent to a reduction of 0.19% clinical mastitis per year. The results show that it is possible to obtain considerable selection response for clinical mastitis, and that selection for increased milk production will result in an unfavorable correlated increase in mastitis incidence, if mastitis is ignored in the breeding program.

(**Key words:** clinical mastitis, protein yield, selection experiment, selection response)

Abbreviation key: CM = clinical mastitis, HMP = high milk production group, HPY = high protein yield group, LCM = low clinical mastitis group, LMP = low milk production group, NRF = Norwegian Dairy Cattle.

INTRODUCTION

Two dairy cattle selection experiments have been carried out in collaboration between GENO Breeding and A. I. Association and the Department of Animal Science, Agricultural University of Norway. In the first experiment, which was carried out from 1978 to 1989, selection was for groups with high (HMP) and low milk production (LMP), respectively. The second experiment began in 1989 and continues today. This experiment includes two groups, selected for high protein yield and low mastitis frequency, respectively. This latter experiment is unique as it is the first selection experiment in dairy cattle with direct selection against clinical mastitis.

In both experiments, sires were selected based on their progeny testing results in the Norwegian Dairy Cattle (NRF) population. For low milk production, a group of 21 sires was initially selected based on their progeny test results in 1978 and 1979; and these bulls were used exclusively during the entire experiment. Otherwise, for each selection group and year, the 2 to 7 highest ranking sires for the respective trait were

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selected from the most recent group of progeny tested bulls. No consideration was made with respect to EBV for other traits. This approach implies single-trait selection of sires, which were preselected for the NRF breeding objective. In NRF, 120 to 130 bulls are progeny tested each year with an average of 250 to 300 daughters per sire. Norwegian dairy cattle have been selected for a broad breeding objective, with steadily increasing emphasis on functional traits like health and fertility over time (Heringstad et al., 2001). The current breeding objective results in genetic improvement of both protein yield and mastitis resistance (Heringstad et al., 2001, 2003), despite the unfavorable genetic correlation between these traits. Heringstad et al. (2000) summarized the estimates of genetic correlation between clinical mastitis and milk production based on Nordic field data and found estimates ranging from 0.24 to 0.55, with an average of 0.43. Recent estimates of the genetic correlation between clinical mastitis and milk production range from 0.25 to 0.45 (Heringstad et al., 1999; Lund et al., 1999; Rupp and Boichard, 1999; Hansen et al., 2002).

Due to the unfavorable genetic correlation between mastitis and milk production, selection for increased milk production is expected to result in a genetic deterioration of mastitis if mastitis is ignored in the breeding program. This response has been confirmed in simulation studies (Strandberg and Shook, 1989; Colleau and le Bihan-Duval, 1995) but never demonstrated with real data, because populations that ignore mastitis in the breeding program generally do not record the trait.

The main objective of this paper was to estimate selection responses for clinical mastitis and protein yield in the two previously described selection experiments. Results from these selection experiments may provide estimation of both the correlated response in clinical mastitis resulting from single trait selection for increased milk production, as well as responses to direct selection against clinical mastitis.

MATERIALS AND METHODS

In both experiments, sires were selected externally from the population at large. To take this factor into account, all available data from the total NRF population from 1978 onward were analyzed with an animal model. The EBV for the cows in the experiments were extracted from these analyses and used for calculation of genetic trends in the selection groups. Results are presented for the two selection experiments and for the entire NRF population. This work represents the first analysis of the NRF population using an animal model.

Selection Experiments

Selection experiment I. The first selection experiment was carried out in the period from 1978 to 1989. Eight herds were included in the experiment (Table 1). Two selection groups were established based on NRF cows present in the herds when the experiment began. Cows were randomly assigned to either a HMP or a LMP group. Each year, the three to seven highest ranking proven sires for milk production were selected from the most recent group of progeny tested NRF sires and mated to the HMP cows (total 49 sires). Sires were used only 1 yr, so very close inbreeding (e.g., father-daughter mating) was therefore avoided. For the LMP group, 21 sires with milk production indices approximately equal to 90 from progeny testing in 1978 and 1979 were selected and used as sires during the entire experimental period. Sires in LMP were used in a rotational system (six to nine sires were used per year) to avoid inbreeding. The milk production index was a relative index with mean 100 and SD 6. Sires were selected based on EBV for 305-d lactation milk production in first lactation, which had been calculated somewhat differently over time (Ødegård, 2000). Until 1978 the selected trait was kg FCM (kg milk $[0.4 + 0.15 \times \text{fat}\%]$). In the period 1979 to 1985, the selection criteria was kg milk, fat percentage, and protein percentage, with twice as much weight on protein percentage as on fat percentage (kg milk $[0.22 + 0.075 \times \text{fat}\% + 0.15 \times \text{protein}\%]$). From 1986 to 1989, the criteria was kg milk with five times as much weight on protein percentage as on fat percentage (kg milk $[0.20 + 0.04 \times \text{fat}\% + 0.20 \times \text{protein}\%]$). In 1989, the selection criterion was changed to 305-d protein yield (kg protein). Directional selection of cows was not practiced in either group. At the end of this experiment, in 1989, most calves and heifers in the LMP group were culled, while animals from HMP were kept in the herds and produced first-lactation records. Therefore, five generations of HMP cows and four generations of LMP cows were included in the analyses.

Cow generation. For these analyses, all cows present in the herds when the selection experiment started, that were mated with one of the defined sires and produced a daughter that made a first lactation record of mastitis and/or protein yield were defined as cow-generation 0. The daughters of these cows were defined as cow-generation 1, and so on. Therefore, cows born in the same year may belong to different cow-generations. Each year, new sires were selected and mated to cows of all generations, so cows in the same cow-generation have sires selected in different years in the HMP group.

Table 1. Number of cows with EBV for clinical mastitis per selection group (HMP = high milk production, LMP = low milk production), cow generation, and herd in selection experiment I.

Herd	Group		Cow generation ¹							Total no. cows
	HMP	LMP	0	1	2	3	4	5	6	
Kalnes	317	313	145	178	162	113	30	2	0	630
Hvam	112	99	51	63	50	30	15	2	0	211
Jønsberg	128	135	56	81	64	46	13	3	0	263
Melsom	162	117	66	87	69	45	12	0	0	279
Åna	392	244	130	185	149	113	49	10	0	636
Øksnevad	126	83	53	73	49	26	6	1	1	209
Gjermundnes	89	48	28	37	34	26	11	1	0	137
Mære	228	129	71	95	88	68	30	5	0	357
Total number of cows	1554	1168	600	799	665	467	166	24	1	2722
Selection group	HMP		311	411	370	311	130	20	1	
	LMP		289	388	295	156	36	4	0	

¹Cow generation = All cows present in the herd when the selection experiment started that were mated with one of the defined sires and produced a daughter that made a first-lactation record of mastitis and/or protein yield were defined as cow generation 0, all their daughters were defined as cow generation 1 and so on.

Selection experiment II. In 1989 another selection experiment was initiated, based mainly on the HMP cows from the first experiment. Eight herds were included: six of the herds from the first experiment and two new school herds (Table 2). Cows were randomly assigned to either a high protein yield (**HPY**) or a low clinical mastitis (**LCM**) group. Each year the 3 to 4 highest ranking proven sires for 305-d protein yield (one selection criterion) were selected from the most recent group of NRF test-bulls and mated to HPY cows. Correspondingly, each year the two to four best proven sires for mastitis resistance (the other selection criterion) were selected and mated to LCM cows. This mating design, corresponding to that of HMP in experiment I, efficiently avoids close inbreeding. As in experiment I, there was no directional selection of cows in either group. Approximately 70% of the cows

in generation 0 were HMP cows from experiment I, 8% were LMP cows, and 22% were other NRF cows (mainly cows in the two new herds). In cow generation 1, 75% of LCM cows and 64% of the HPY cows had mothers from HMP. Three generations of cows had completed first lactation at the time of these analyses. This experiment is ongoing.

Data

NRF population. Data were extracted from a research database containing all phenotypic information from the Norwegian Dairy Herd Recording System since 1978. The mastitis data file included information regarding clinical mastitis (**CM**) during first lactation for all cows with date of first calving between September 1st 1978 and September 1st 1998. A record

Table 2. Number of cows with EBV for clinical mastitis per selection group (HPY = high protein yield, LCM = low clinical mastitis), cow generation, and herd in selection experiment II.

Herd	Group		Cow generation ¹					Total number of cows
	HPY	LCM	0	1	2	3	4	
Kalnes	200	173	122	151	84	16	0	373
Jønsberg	51	58	35	48	21	5	0	109
Valle	119	68	65	73	44	5	0	187
Buskerud	68	55	39	50	31	3	0	123
Åna	185	201	102	153	109	22	0	386
Øksnevad	81	58	46	55	31	7	0	139
Gjermundnes	37	43	19	31	24	5	1	80
Mære	107	86	58	76	49	10	0	193
Total number of cows	848	742	486	637	393	73	1	1590
Selection group	HPY		260	345	208	35	0	
	LCM		226	292	185	38	1	

¹Cow generation = All cows present in the herd when the selection experiment started that were mated with one of the defined sires and produced a daughter that made a first-lactation record of mastitis and/or protein yield were defined as cow-generation 0, all their daughters were defined as cow generation 1 and so on.

Table 3. Summary statistics of the datasets used for prediction of breeding values for clinical mastitis and protein yield.

	Clinical mastitis	Protein yield
Cows with data, no.	2,033,941	1,576,579
Herds, no.	29,055	29,158
Herd × year classes, no.	413,210	412,972
Mastitis frequency ¹ , %	15.0	
Mean 305-d protein yield ² , kg		170.1
SD 305-d protein yield ² , kg		34.9
Animals in the pedigree file, no.	2,316,164	1,897,747
Base animals in the pedigree file, no.	86,417	70,984

¹Mastitis frequency = Percentage of cows with at least one record of veterinary treated clinical mastitis in the period from 15 d before to 120 d after first calving.

²Only cows with complete 305-d lactation were included.

was included if age of first calving was between 450 and 1200 d and the lactation began with a normal calving. To ensure participation in the health recording system, only cows from herds with at least one health recording during the year the cow calved were included. Mastitis was defined as a binary trait based on whether or not the cow had at least one case of veterinary treated CM in the period from 15 d before to 120 d after first calving. This definition is the same as currently used for genetic evaluation of the trait in NRF. The resulting file contained CM information for 2,033,941 cows and the average CM frequency was 15% (Table 3). Data on 305-d protein yield in first lactation were extracted using the same criteria for calving period, age of first calving, and start of lactation as for CM. Only cows with complete 305-d lactation records were considered. Mean and SD of 305-d protein yield was 170.1 and 34.9, respectively (Table 3). The resulting file contained information on 305-d protein yield for 1,576,579 cows (Table 3). The structure of the data sets is shown in Table 3.

Selection experiment I. A total of 2496 cows from experiment I had first-lactation CM records, including 1427 HMP cows and 1069 LMP cows (Table 4). The

average mastitis frequencies were 18.3% for HMP cows and 12.8% for LMP cows (Table 4). A total of 1815 cows, 1098 from the HMP group, and 717 from the LMP group, completed 305-d of first lactation (Table 4). The average 305-d protein yields were 185.1 kg and 165.1 kg for HMP and LMP cows, respectively (Table 4). A total of 2722 cows had EBV for CM, and the numbers per herd, selection group and cow-generation are given in Table 1.

Selection experiment II. A total of 1566 cows in experiment II had first lactation CM records, of which 831 were HPY cows and 735 were LCM cows. Mean frequencies of CM were 15.2 and 15.0% for HPY and LCM, respectively (Table 4). A total of 1117 cows, 610 from the HPY group and 507 from the LCM group, completed 305-d of first lactation, with a mean 305-d protein yield of 185.9 kg for HPY cows and 178.5 kg for LCM cows (Table 4). A total of 1590 cows had EBV for CM, distributed over selection groups, cow-generations, and herds as shown in Table 2.

Pedigree File

The initial pedigree file for the NRF population included 3.7 million records. From this file, separate

Table 4. Summary statistics for high milk production (HMP) and low milk production (LMP) group cows from selection experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) group cows from selection experiment II.

	Selection group			
	HMP	LMP	HPY	LCM
Cows with first-lactation clinical mastitis observation	1427	1069	831	735
Cows with EBV for clinical mastitis	1554	1168	848	742
Mastitis frequency, ¹ %	18.3	12.8	15.2	15.0
Cows with first lactation 305-d protein yield observation ²	1098	717	610	507
Cows with EBV for 305-d protein yield	1306	871	671	560
Mean 305-d protein yield, kg	185.1	165.1	185.9	178.5
SD 305-d protein yield, kg	30.9	30.4	34.8	34.5
Sires, no.	49	21	24	17

¹Mastitis frequency = Percentage of cows with at least one record of veterinary treated clinical mastitis in the period from 15 d before to 120 d after first calving.

²Only cows with complete 305-d lactation were included.

Figure 1. Mean mastitis frequency, as percentage of cows with at least one case of clinical mastitis (CM) in the period from 15 d before to 120 d after first calving, per cow generation in two selection experiments, with high milk production (HMP) and low milk production (LMP) groups in experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) groups in experiment II.

pedigree files for the cows in the CM and protein yield datasets were derived by tracing the pedigrees for cows with data back as far as possible. The resulting pedigree files had 2,316,164 (CM) and 1,897,747 (protein yield) observations, respectively (Table 3). A total of 3.7% of the animals in the pedigree-files were base animals.

Model

Breeding values for CM were calculated using the following linear model:

$$Y_{ijkl} = A_i + M_j + HY_k + a_l + e_{ijkl}$$

where

Y_{ijkl} = observation of CM (0 = healthy, 1 = diseased) for cow l , calving at age i , in month j , and herd $\times$ year class k ;

A_i = fixed effect of age at calving i in 15 classes, where <20 mo is the first class, >32 mo the last class, and the other classes are in single months;

M_j = fixed effect of month of calving j in 12 classes;

HY_k = fixed effect of herd-year class k ;

a_l = random effect of animal l ; and

e_{ijkl} = random error term.

Protein yield was analyzed using the model:

$$Y_{ijklm} = A_i + M_j + DO_k + HY_l + a_m + e_{ijklm}$$

where

Y_{ijklm} = observation of 305-d protein yield (kg protein) for cow m , calving at age i , in month j , and herd $\times$ year class k and herd $\times$ year class l ;

DO_k = fixed effect of days open class k in 14 classes, where <30 d is the first class, >149 d is the last class, and the other classes are in 10 d intervals; and

other effects were as defined previously for CM.

The models included the same fixed effects as the linear sire models used by Heringstad et al. (1999; 2001). Univariate analyses were chosen because a previous study (Heringstad et al., 2001) showed that estimates of genetic trends in this population were the same from univariate analyses and bivariate analysis of CM and protein yield.

Variance components for CM and 305-d protein yield were estimated with VCE4 (Neumaier and Groeneveld, 1998) using linear sire models with the same fixed effects as described above and data restricted to daughters of sires progeny tested in the years from 1978 to 1998. The resulting sire (σ_s^2) and residual (σ_{e-s}^2) variances were used to calculate variance components relevant for the animal model as follows:

$$\sigma_a^2 = 4\sigma_s^2 \text{ and } \sigma_e^2 = \sigma_{e-s}^2 - 3\sigma_s^2.$$

Additive relationship matrices were included in the analyses, and breeding values were estimated using the program PEST (Groeneveld and Kovac, 1990).

Genetic trends were estimated by linear regression of EBV on cow generation and cows birth-year, and t -tests were used to test whether the regression coefficients were different from zero and to assess whether mean EBV were significantly different between selection groups for each cow generation.

Table 5. Mean EBV for clinical mastitis (EBV_{CM}) and 305-d protein yield (EBV_{PY}) of sires mated to high milk production (HMP) or low milk production (LMP) group cows in selection experiment I, per year and selection group.

Year	HMP			LMP		
	No. sires	Mean EBV _{CM}	Mean EBV _{PY}	No. sires	Mean EBV _{CM}	Mean EBV _{PY}
1978	7	0.0268	11.53	9	-0.0147	-8.66
1979	4	0.0468	16.17	12	-0.0009	-11.48
1980	6	-0.0178	7.17			
1981	7	0.0108	4.34			
1982	3	0.0816	7.78			
1983	3	0.0536	11.18			
1984	3	0.0026	10.89			
1985	3	0.0285	15.51			
1986	3	0.0472	15.66			
1987	3	-0.0142	13.25			
1988	4	0.0532	19.32			
1989	3	0.0415	21.30			

RESULTS AND DISCUSSION

Figure 1 shows mean mastitis frequency per cow generation in the two selection experiments. Cows in the LMP group show a relatively flat phenotypic trend, whereas mastitis frequency in the HMP group increased with cow generation. In selection experiment II, mastitis frequency decreased in the LCM group and increased somewhat for the HPY group. Phenotypic mastitis frequency in cow generation 0 was higher in the LCM group than in the HPY group.

The variance components for animal (σ_a^2) and residual (σ_e^2) effects were 0.0038 and 0.1198 for CM, and 100.8 and 427.2 for 305-d protein yield, corresponding to heritabilities of 0.03 and 0.19, respectively. The overall mean (SD) EBV for CM and 305-d protein yield in the total dataset were 0.002 (0.029) and 3.07 (6.28), respectively. Annual mean EBV for CM and 305-d protein yield for sires used in the two experiments are given in Tables 5 and 6.

Mean EBV for CM in the two selection experiments are given in Figure 2. The genetic trend for LMP cows was flat, while mean EBV for CM in the HMP group increased with cow generation. Mean EBV was significantly different ($P < 0.0001$) between the two selection groups from cow generation 1 onwards. The genetic difference in CM between HMP and LMP cows in experiment I, equivalent to 3.1% CM after four cow-generations, is most likely a correlated response in CM after selection for increased milk production in the HMP group. In selection experiment II, the genetic level of CM in cow generation 0 was the same for the two groups (Figure 2). The genetic trend of CM was approximately flat for HPY cows and strongly decreasing in the LCM group. Mean EBV was significantly different ($P < 0.0001$) in HPY and LCM from cow generation 1 onwards. Here, the genetic difference of 8.6% CM after three cow generations is mainly a result of direct selection against CM in the LCM group.

Linear regression analyses of EBV for CM on cow generation indicated a genetic increase of 0.78% and

Table 6. Mean EBV for clinical mastitis (EBV_{CM}) and 305-d protein yield (EBV_{PY}) of sires mated to high protein yield (HPY) and low clinical mastitis (LCM) group cows, in selection experiment II, per year and selection group.

Year	HPY			LCM		
	No. of sires	Mean EBV _{CM}	Mean EBV _{PY}	No. of sires	Mean EBV _{CM}	Mean EBV _{PY}
1989	3	0.0415	21.30	2	-0.0772	-2.82
1990	3	0.0016	19.91	2	-0.0773	-0.02
1991	4	0.0535	24.79	2	-0.0622	-8.66
1992	3	0.0156	23.82	2	-0.1071	8.27
1993	3	0.0059	26.15	3	-0.0575	3.76
1994	4	0.0261	21.54	3	-0.0928	2.78
1995	4	0.0425	26.30	3	-0.0596	5.79
1996	3	-0.0341	27.70	3	-0.0626	1.32
1997	4	0.0056	22.81	4	-0.0678	1.79
1998	3	0.0021	29.90	4	-0.0748	9.39

Figure 2. Mean EBV for clinical mastitis (CM) per cow generation for cows in two selection experiments, with high milk production (HMP) and low milk production (LMP) groups in experiment I, and high protein yield (HPY) and low mastitis frequency (LCM) groups in experiment II.

0.24% CM per cow generation for HMP and HPY cows, respectively (Table 7). A genetic improvement equivalent to a reduction of 3.03% CM per cow generation was estimated for the LCM group, and an approximately flat genetic trend was found for the LMP group (Table 7). The regression coefficients for HMP and LCM were significantly different from zero ($P < 0.0001$), whereas the levels of significance were 0.058 and 0.173 for HPY and LMP, respectively (Table 7).

Mean EBV for CM per birth-year in the NRF population and for selection groups in the two experiments

are given in Figure 3. Genetic trend for CM in the NRF population was approximately flat for cows born before 1990 and slightly decreasing thereafter. The corresponding regression coefficients indicate a genetic change of +0.04% CM per year from 1976 to 1990, and -0.19% CM per year from 1990 onwards (Table 7). This agreed closely with Heringstad et al. (2003) who found a similar result using linear and threshold sire models. However, the estimate of annual genetic change after 1990 was slightly lower from the animal model (-0.19% CM) than the estimate of Heringstad

Table 7. Regression coefficients from linear regression analysis of EBV for clinical mastitis (EBV_{CM}) and 305-d protein yield (EBV_{PY}) on cow generation and birth-year of cow, respectively, for high milk production (HMP) and low milk production (LMP) group cows from selection experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) group cows from selection experiment II, and for the entire Norwegian Dairy Cattle (NRF) population.

Dependent variable	Independent variable	Group	Generation/period	Regression coefficient ¹	P-value ²
EBV_{CM}	Cow generation ³	HMP	0–5	0.78	<0.0001
		LMP	0–4	0.08	0.173
		HPY	0–3	0.24	0.058
		LCM	0–3	-3.03	<0.0001
	Birth-year cow	HMP	1976–1990	0.23	<0.0001
		LMP	1976–1990	-0.02	0.307
		HPY	1987–1996	0.04	0.317
		LCM	1987–1996	-0.91	<0.0001
		NRF	1976–1996	-0.01	<0.0001
		NRF	1976–1990	0.04	<0.0001
		NRF	1990–1996	-0.19	<0.0001
		NRF	1976–1996	-0.19	<0.0001
EBV_{PY}	Cow-generation ³	HMP	0–5	3.23	<0.0001
		LMP	0–4	-2.83	<0.0001
		HPY	0–3	4.85	<0.0001
		LCM	0–3	-1.97	<0.0001
	Birth-year cow	HMP	1976–1990	1.00	<0.0001
		LMP	1976–1990	-0.87	<0.0001
		HPY	1987–1996	1.40	<0.0001
		LCM	1987–1996	-0.50	0.0003
		NRF	1976–1996	0.47	<0.0001

¹For CM: Regression coefficient $\times 100$ (equivalent to % CM).

²For hypothesis, regression coefficient = 0.

³Cow generation = All cows present in the herd when the selection experiment started that were mated with one of the defined sires and produced a daughter that made a first-lactation record of mastitis and/or protein yield were defined as cow-generation 0, all their daughters were defined as cow-generation 1 and so on.

Figure 3. Mean EBV for clinical mastitis (CM) by birth-year for the Norwegian Dairy Cattle (NRF) population and for cows in two selection experiments; with high milk production (HMP) and low milk production (LMP) groups in experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) groups in experiment II.

et al. (2003) from a linear sire model (-0.23% CM). The genetic trend may have been somewhat over estimated with the sire model. Genetic improvement implies that the mean genetic level of the mothers of the daughters used to predict sire EBV increases over time, while the sire model assumes that sires are mated to cows at random, i.e., to cows with a constant genetic level over time. On the other hand, Heringstad et al. (2003) compared genetic change estimates from linear and a threshold sire model, and concluded that given that the threshold model holds true, the magnitude of genetic change for CM was slightly understated by the linear sire model in these data. The annual genetic response may therefore also have been underestimated with the linear animal model used in the present study.

The genetic trend of CM was larger in HMP than in HPY (Figures 2 and 3). In these experiments, sires were from the NRF population, which has changed genetically over time (Figure 3). The difference in genetic trends of CM between the HMP and HPY groups, both selected for increased milk production, can probably be explained by this preselection. The genetic trend for CM in the HPY group is thus not representative for what would happen in a population selected only for increased production. Rather, the difference between genetic trends for CM in the NRF population and in the HPY group describe the indirect selection response in CM resulting from selection for increased milk production.

In the time period when the genetic trend of CM in the NRF population was approximately flat, a genetic increase equivalent to 0.23% CM per year was found for HMP cows, while in the period where the NRF population showed a genetic improvement of -0.19% CM per year an approximately flat genetic trend

($+0.04\%$ CM per year) was found for HPY cows (Figure 3 and Table 7). The difference between genetic trend for CM in the NRF population and in the groups selected for increased milk yield, HMP and HPY, respectively, indicates that an increase between 0.19 and 0.23% CM per year may be expected as a correlated response to selection for increased milk production in NRF, given that similar selection intensities are used.

Our study is the first to quantify the correlated genetic change in CM resulting from selection on increased milk production. The results, however, agree with results from several other designed experiments reporting increased health costs as a correlated response to selection for increased milk yield (Hansen et al., 1979; Bertrand et al., 1985; Short et al., 1990; Dunklee et al., 1994; Jones et al., 1994). From a selection herd in Minnesota, Hansen et al. (1979) reported increased labor and health care expenses for cows in a group selected for high milk yield compared with cows in the control group. In the same herd Jones et al. (1994) compared health care costs for cows born from 1975 to 1990 and found that cows in the selection group had higher health expenses as a correlated response to increased milk yield than did unselected controls, and that expenses due to mastitis accounted for most of the difference between groups. Dunklee et al. (1994) evaluated a selection experiment with Holstein cows that included two groups with high and average milk yield, respectively. They reported that the high yielding cows had higher total health costs and higher mammary health costs than did the cows in the average yield group. The mean number of cases of mastitis per lactation was 0.46 in the high yield group and 0.29 in the average yield group. Bertrand et al. (1985) reported that daughters of high Predicted Difference Milk sires produced 16% more milk, had 26% more mammary costs, and 42% more discarded milk costs, than daughters of breed average sires. Also significant differences in health costs found between a line of Jersey cows selected for milk yield and a control line were mainly due to higher mammary health costs (Short et al., 1990).

Mean EBV for 305-d protein yield per cow generation in the two selection experiments are given in Figure 4. The difference between selection groups was significantly different ($P < 0.0001$) after cow generation 0 in both experiments. The HMP and HPY groups showed as expected a positive genetic trend for protein yield, with a genetic gain of 3.23 and 4.85 kg protein per cow generation (Table 7). In the LMP and LCM groups the genetic trends were negative, corresponding to a genetic change of -2.83 and -1.97 kg protein per cow generation (Table 7). All these regressions of EBV for 305-d protein yield on cow generation were

Figure 4. Mean EBV for 305-d protein yield (PY) per cow generation for cows in two selection experiments; with high milk production (HMP) and low milk production (LMP) groups in experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) groups in experiment II.

significantly different from zero ($P < 0.0001$) (Table 7). In Figure 5, mean EBV for 305-d protein yield are given by birth-year for cows in the two selection experiments and also for the NRF population. The figure shows a positive genetic trend for protein yield in the NRF population, as well as for the HMP and HPY groups. The trend for the LCM group was negative, but varied as expected between years, since mean EBV for 305-d protein yield of the sires used in LCM varied strongly between years (Table 6). The negative genetic trend for protein yield in the LCM group is most likely a correlated response after selection against CM, due to the unfavorable genetic correlation between the two traits.

The annual genetic trend in the NRF cow population of 0.47 kg protein per year (Table 7), expected to be approximately one-half the genetic trend for AI sires, agree with Heringstad et al. (2001). They reported an annual genetic improvement of 0.96 kg protein per year for NRF sires born between 1974 and 1990, based on a linear regression analysis of sire EBV for 305-d protein yield on sires birth-year. The annual genetic

Figure 5. Mean EBV for 305-d protein yield (PY) per birth-year for the Norwegian Dairy Cattle (NRF) population and for cows in two selection experiments; with high milk production (HMP) and low milk production (LMP) groups in experiment I, and high protein yield (HPY) and low clinical mastitis (LCM) groups in experiment II.

trend in the groups selected for increased milk production, HMP and HPY, was lower than the genetic trends for milk yield of US Holsteins, which according to a review by Hansen (2000) were 79, 102, and 116 kg/yr during the 1970s, 1980s, and in the period from 1990 to 1996, respectively (corresponding to between 2.5 and 3.7 kg protein per year). Selection in the HMP and HPY groups were not strict single trait selection. Although sires were selected solely based on their breeding values for milk production, they were selected among progeny-tested bulls and therefore had been preselected for NRF breeding objective with increasing weight on health and fertility over the last 20 yr.

CONCLUSIONS

The results from the two selection experiments clearly demonstrate the effect of direct and indirect selection on CM. The genetic trend for LCM cows shows that considerable selection response can be achieved for CM if sufficient selection pressure is put on the trait. On the other hand, if mastitis is ignored in the breeding program, selection for increased milk production will result in an unfavorable correlated selection response in CM, as illustrated by the genetic trend for CM for HMP cows. Results for the NRF population shows that it is possible to obtain genetic improvement for both CM and protein yield simultaneously, if the traits are recorded for large daughter groups and given sufficient weight in selection.

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