Genetic Analysis of the Israeli Holstein Dairy Cattle Population for Production and Nonproduction Traits with a Multitrait Animal Model

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ABSTRACT

Milk, fat, and protein production, somatic cell score (SCS), and female fertility in the Israeli Holstein dairy cattle population were analyzed using a multitrait animal model (AM) with parities 1 through 5 as separate traits. Female fertility was measured as the inverse of the number of inseminations to conception in percent. Variance components were estimated using both the repeatability AM and multitrait AM. The multitrait heritabilities for individual parities were greater than the heritabilities from the repeatability AM, and heritabilities decreased with an increase in parity number. Heritabilities were higher for production traits, lower for SCS, and lowest for female fertility. The genetic correlations were higher than the environmental correlations. Genetic correlations between parities decreased with an increase in the difference in parity number, but all were greater than 0.5. The environmental correlations were higher for production traits, lower for SCS, and close to zero for female fertility. In the analysis of the complete milk recorded population, genetic trends from the repeatability and multitrait models were very similar. The genetic trend for SCS was economically unfavorable until 1993, and favorable since then. The genetic trend for female fertility was close to zero, but the annual environmental trend was -0.2% . The multitrait lactation model is an attractive compromise between repeatability lactation models, which do not account for maturing trends across parities, and test-day models, which are much more demanding computationally.

(Key words: multitrait animal model, Israeli Holsteins, records in progress-dip, genetic evaluation)

Abbreviation key: AM = animal model, BVT = total breeding value, RIP = records in progress.

INTRODUCTION

Various methods have been proposed for routine genetic evaluation of dairy cattle for economically important traits. Until 1988 sire models were the method of choice. With the increase in computing capabilities in the 1980s, animal models (AM) became computationally feasible even for the largest commercial populations (VanRaden and Wiggans, 1991). Early AM generally included records from multiple parities, but were single-trait or “repeatability” models. That is, genetic correlations of unity between parities were assumed, even though numerous studies have shown that this is not the case for milk production traits (e.g., Albuquerque et al., 1996). A “permanent environmental” factor was included to account for similarities between multiple records of the same animal that were not due to additive genetic factors.

Jamrozik et al. (1997) noted that if incomplete evaluations are included in a lactation model analysis, differences in persistency of production during the lactation can cause the “RIP-dip” (records in progress “dip”) (RIP) phenomenon; the often-observed reduction in the genetic evaluation of elite sires that are returned to general service, based on their genetic evaluations from the first daughter crop. If first and later parities are included in the analysis, RIP-dip could also be caused by incomplete genetic correlations among parities. In an analysis of 16 AI bulls that were progeny tested and returned to general service in Israel between 1993 and 2001, there was a reduction in the mean of the evaluations of 169 kg of milk, 3 kg of fat, and 2.7 kg of protein between the original evaluation, and the first evaluation after the bull was returned to general service (Weller and Ezra, 2001). Both sets of evaluations were by the repeatability AM. If the genetic value of a particular sire increases from parity to parity, then his evaluation will also increase as the daughters from the first crop age. However, once the sire is returned to general service, the large number of new first-parity records will overwhelm the relatively small number of test-day rec-

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ords from the first daughter crop, and his evaluation will decline. An opposite effect would be observed for sires with decreasing genetic evaluations.

Da and Grossman (1991) presented equations for genetic analysis by a multitrait AM, including genetic groups for animals with incomplete pedigree information. In a repeatability AM, the number of equations that must be solved will be equal to approximately twice the number of animals included in the analysis. In the multiparity multitrait AM (henceforth "multitrait AM"), the number of equations will be approximately equal to the number of animals times the number of parities included in the analysis. Thus, most previous commercial multitrait AM evaluations have included a maximum of 3 parities, and a large fraction of the production records are discarded. With current computing facilities available, this restriction is no longer necessary, and even 5 parities can be readily analyzed for large dairy cattle populations.

In addition to milk, fat, and protein production, the multitrait AM is also appropriate for analysis of other traits, for which the individual parity records are genetically correlated, but correlations are less than unity; such as SCS and female fertility. Previous studies have estimated genetic parameters for first through third parities for production traits by multitrait AM, (e. g., Albuquerque et al., 1996). The objectives of this study were:

- To compute the genetic parameters required for the multitrait AM analyses of milk, fat, protein, SCS, and female fertility, including parities 1 through 5.
- To compute the genetic evaluations for these 5 traits for all milk-recorded animals included in the Israeli-Holstein population, and compare the multitrait AM evaluations to the repeatability AM evaluations.
- To estimate genetic trends for these 5 traits by repeatability and multitrait AM.

MATERIALS AND METHODS

Trait Definitions

The 305-d milk, fat, and protein yield, and lactation measures of SCS and female fertility were analyzed. Milk, fat, and protein yield were adjusted for days open, calving age and month, and parity using multiplicative factors as described by Ezra et al. (1987). Edits on milk production records were as described by Weller and Ezra (1997). Milk production records were included if there were at least 2 valid monthly tests, the first

Table 1. Phenotypic means and standard deviations for the traits analyzed in the entire Israel Holstein population.¹

Trait	Mean	Standard deviation
Milk yield (kg)	10,281	1718
Fat yield (kg)	331	64
Protein yield (kg)	311	50
Percent fat	3.23	0.42
Percent protein	3.04	0.19
SCS ²	4.94	1.33
Female fertility (%) ³	50.6	34.5

¹Valid lactation records since January 1, 1985. All records are adjusted, as described in the text.

²Corrected mean of log₂ scores (Weller and Ezra, 1997).

³As computed by Weller and Ezra (1997).

monthly test was <65 DIM, and the difference between first 2 consecutive tests was <75 d. Incomplete records were extended, as described by Weller (1988). Production records were included only if there were valid records for all 3 milk production traits. Thus, the number of records and the number of levels of factors were the same for the 3 production traits in all analyses. The lactation measure of SCS was the mean of the lactation SCS scores, corrected for DIM and parity (Weller and Ezra, 1997). Lactations with less than 4 valid SCS were deleted. The lactation measure of female fertility was the inverse of the number of inseminations to conception in percent (Weller and Ezra, 1997). If conception was not recorded, the expected number of inseminations to conception was computed by summing the product of the insemination number and the probability of conception at that insemination from the recorded number of inseminations + 1 through 13. The summation up to 13 was arbitrary, but preliminary studies showed that increasing this value did not significantly affect the expectation (Weller and Ezra, 1997). Lactation records of cows that were not inseminated were deleted. Additional edits and correction factors for both SCS and female fertility were as described by Weller and Ezra (1997). The means and standard deviations for the traits analyzed for the entire milk recorded population are given in Table 1.

Estimation of Variance Components

Variance components were estimated for both the repeatability and multitrait AM by the MTC REML program (Misztal, personal communication). The repeatability AM analyses included first through fifth parities of all milk-recorded cows with valid first-parity lactations and freshening dates between April 1, 1994, and March 31, 1996. Thus, by 2002, all cows could have produced 5 lactations, unless culled. Later-parity lactations were included if there were valid records for all

Table 2. Number of levels of the factors included in the analysis models.

Analysis	Factor	Trait		
		Production ¹	SCS	Fertility
REML, repeatability model	Herd-year-seasons	9881	10,338	9,438
	Groups	2	2	2
	Cows with records	59,536	56,610	50,843
	Total animals	110,109	105,097	94,934
	Records	158,501	156,085	126,136
REML, multitrait	Herd-year-seasons	6244	5490	3250
	Groups	2	2	2
	Cows with records	28,769	20,169	20,203
	Total animals	52,194	37,806	37,148
	Records	158,501	156,085	126,136
Complete population ²	Herd-year-seasons	25,006	21,577	27,576
	Genetic groups	58	55	68
	Parity by management group	20	30	10
	Cows with records	431,242	310,157	413,103
	Cows without records	92,805	121,955	87,200
	Bulls	1,468	1,342	1,422
	Records	1,050,566	723,219	1,004,215
	Records	1,050,566	723,219	1,004,215

¹Milk, fat, and protein yield. Number of records and levels of factors were the same for these 3 traits.

²Number of records and levels of factors were the same for both the repeatability and multitrait animal models.

previous lactations. Thus the number of lactations per cow could vary from 1 through 5. The analysis model for all 5 traits was:

$$Y_{ijklm} = H_{ij} + G_{ik} + A_{il} + P_{il} + e_{ijklm},$$

where Y_{ijklm} = the record for parity m of cow l from herd-year-season j for trait i ; H_{ij} = the effect of herd-year-season j on trait i ; G_{ik} = the effect of genetic group k on trait i ; A_{il} = the additive genetic effect of cow l for trait i ; P_{il} = the permanent environmental effect of cow l for trait i ; and e_{ijklm} = random residual.

The H and G effects were considered fixed, all other effects were assumed to be random, and variance components were estimated. Two seasons were defined for each herd year based on calving date, from April 1 through September 30, and from October 1 through March 31. Two genetic groups were defined for animals with unlisted parents using the method of Westell et al. (1988), group 1 for animals with one unlisted parent and group 2 for animals with both parents unlisted. The relationship matrix, including all known relationships among cows and bulls was included in the analysis model. Parents and grandparents of cows with records, and grandparents of sires of cows with records were included in the relationship matrix. The numbers of records and level of the effects are given in Table 2 for all 5 traits.

For the multitrait REML analysis, only cows with valid records for all 5 parities were included. This is a requirement of the REML program used. Therefore, for the milk production traits, cows with first-parity

freshening dates between April 1, 1990, and March 31, 1996, were included in the analysis. For SCS and female fertility, for which fewer valid records were available, cows with first-parity freshening dates between April 1, 1988, and March 31, 1996, were included in the analyses. The analysis model was:

$$Y_{ijklm} = H_{ij} + G_{ikm} + A_{ilm} + e_{ijklm},$$

where G_{ikm} = the effect of genetic group k on parity m for trait i ; A_{ilm} = the additive genetic effect of cow l on parity m for trait i ; and the other terms are as defined previously. This model does not include a permanent environmental effect for each cow. Instead, environmental covariances are estimated among the 5 parities. The H and G effects were defined the same as for the repeatability AM, and ancestors were included using the same criteria. The numbers of records and level of the effects are also given in Table 2 for all 5 traits.

Analysis of the Entire Milk-Recorded Population

The entire milk-recorded Israeli-Holstein population including all cows with first-parity freshening dates since January 1, 1985, was analyzed by both the repeatability and multitrait models for all 5 traits. Milk production records were included if the freshening date was prior to June 1, 2002, with additional edits as described previously. Somatic cell score records were included if the freshening date was prior to April 1, 2002, and there were at least 4 valid SCS records during the lactation. Female fertility records were included if the

freshening date was prior to March 1, 2002, and the cow was inseminated at least once during the lactation. For all 3 analyses, later-parity records were included only if there were valid records for all previous parities. Thus the number of records per cow could vary from zero to 5.

The same statistical models were used, except that in both cases a herd management $\times$ parity effect was included, as proposed by Wiggans and VanRaden (1994), and more groups were defined. Cows of different parities were included in the same herd-year-season. Thus even though a global multiplicative adjustment for parity was applied, there could still be a potential bias, if parity effects changed over time or management type, unless a parity effect was included in the model. Two herd management types were defined, family farms with <100 cows/herd, and communal herds with >100 cows/herd. Generally cows at family farms are milked twice daily, and cows at communal herds are milked 3 times daily. Cows were grouped by management type, because preliminary results showed that parity effects were not equal for the 2 management types. For the milk production traits, the 2 management types were further divided into 2 groups based on the cows' first-parity freshening date. Thus, there were 20 herd management $\times$ parity levels for each trait. For SCS the management types were divided into 3 groups based on the cows' first-parity freshening date, because management by parity changes relative to this trait were more significant. Prior to 1990, there was no penalty for high SCC, and since then penalties have varied over time. Thus, there were 30 management $\times$ parity levels for this trait. For female fertility, only 2 management groups were defined based on the cows' first-parity freshening date. Communal and family farms were combined, because there were very few valid records from family farms in the early years. Thus only 10 levels were defined for this trait.

Genetic groups were determined separately for bulls and cows with unrecorded parents, using the method of Westell et al. (1988). For each sex, groups were determined based on the animals' birth year, and which parents (sire, dam, or both) were unrecorded. Considering the relatively small number of bulls with unrecorded parents, it was not possible to apply additional grouping criteria, such as country of origin. Reliabilities of the repeatability AM evaluations were estimated using the algorithm of Misztal and Wiggans (1988), as corrected by Misztal et al. (1991).

The genetic base for the evaluations of all traits was the mean value of cows born in 1995. For the multitrait analyses, the individual parity breeding values of each trait were combined into a single total evaluation (**BVT**) by the following equation:

Table 3. Relative variance components for the repeatability animal model analyses.

Trait	Genetic	Permanent environment	Residual
Milk	0.285 (0.250) ¹	0.216 (0.250)	0.499 (0.500)
Fat	0.293 (0.250)	0.206 (0.250)	0.501 (0.500)
Protein	0.276 (0.250)	0.200 (0.250)	0.524 (0.500)
SCS	0.108 (0.100)	0.134 (0.250)	0.757 (0.650)
Female fertility	0.024 (0.025)	0.058 (0.075)	0.918 (0.900)

¹The variance components used in the repeatability animal model analysis of the complete population are given in parenthesis.

$$\text{BVT} = (\text{BV}_1 + 0.73\text{BV}_2 + 0.51\text{BV}_3 + 0.34\text{BV}_4 + 0.21\text{BV}_5)/2.79,$$

where BV_1 to BV_5 are the individual parity breeding values. The coefficients relative to first parity were derived based on the probability that the cow would produce a record in each parity times the discounted value of each parity. A 5% discounting factor was assumed for each additional parity after first.

Breeding values for fat and protein percentage, BVPF and BVPP, were computed as follows:

$$\text{BVPF} = 100[(343 + \text{BVF})/(10,707 + \text{BVM}) - 343/10,707]$$

$$\text{BVPP} = 100[(319 + \text{BVP})/(10,707 + \text{BVM}) - 319/10,707]$$

where BVF, BVP, and BVM are the breeding values for fat, protein, and milk yield. The values 343, 319, and 10,707 are mean kilograms of fat, protein, and milk yield in the base year of 1995.

Genetic trends were computed as the regression of the cows' estimated breeding values on their birth dates for cows born between 1981 and 2000. Genetic trends were computed for the repeatability AM, the multiparity AM individual parity evaluations, and the multiparity AM index. First-parity phenotypic trends were computed as the regression of the cows' first-parity phenotypic record on their birth dates. First-parity environmental trends were computed as the difference of the phenotypic and genetic trends. Correlations between the repeatability AM evaluations and multitrait AM index were computed for sire evaluations with repeatability values greater than 0.5.

RESULTS AND DISCUSSION

The variance components from the repeatability AM analyses are presented in Table 3 for all 5 traits. The variance components used in the repeatability AM analyses of the complete population are given in parenthesis. These are the variance components used in the official national evaluations and are similar to those estimated by the REML analyses. In general, the heri-

Table 4. Genetic and environmental correlations and heritabilities for milk yield from the multitrait animal model.¹

	Parities				
	1	2	3	4	5
1	0.39	0.89	0.88	0.82	0.74
2	0.57	0.29	0.98	0.92	0.85
3	0.53	0.59	0.27	0.98	0.94
4	0.46	0.53	0.59	0.22	0.98
5	0.32	0.37	0.44	0.51	0.12

¹Genetic correlation are above the diagonal, environmental correlations are below the diagonal, and heritabilities are on the diagonal in bold type.

Table 5. Genetic and environmental correlations and heritabilities for fat yield from the multitrait animal model.¹

	Parities				
	1	2	3	4	5
1	0.42	0.91	0.88	0.84	0.76
2	0.58	0.38	0.99	0.96	0.90
3	0.53	0.61	0.34	0.99	0.95
4	0.46	0.55	0.59	0.29	0.98
5	0.34	0.41	0.47	0.52	0.20

¹Genetic correlation are above the diagonal, environmental correlations are below the diagonal, and heritabilities are on the diagonal in bold type.

Table 6. Genetic and environmental correlations and heritabilities for protein yield from the multitrait animal model.¹

	Parities				
	1	2	3	4	5
1	0.34	0.89	0.85	0.77	0.67
2	0.54	0.29	0.98	0.92	0.83
3	0.48	0.59	0.27	0.98	0.91
4	0.41	0.52	0.59	0.23	0.97
5	0.28	0.43	0.43	0.52	0.15

¹Genetic correlation are above the diagonal, environmental correlations are below the diagonal, and heritabilities are on the diagonal in bold type.

Table 7. Genetic and environmental correlations and heritabilities for SCS from the multitrait animal model.¹

	Parities				
	1	2	3	4	5
1	0.25	0.85	0.84	0.82	0.81
2	0.31	0.22	0.98	0.95	0.93
3	0.26	0.44	0.23	0.99	0.97
4	0.24	0.37	0.48	0.23	0.99
5	0.23	0.33	0.40	0.49	0.18

¹Genetic correlation are above the diagonal, environmental correlations are below the diagonal, and heritabilities are on the diagonal in bold type.

Table 8. Genetic and environmental correlations and heritabilities for female fertility from the multitrait animal model.¹

	Parities				
	1	2	3	4	5
1	0.02	0.74	0.86	0.66	0.54
2	0.05	0.03	0.82	0.94	0.79
3	0.05	0.05	0.02	0.88	0.75
4	0.04	0.05	0.06	0.03	0.92
5	0.05	0.06	0.08	0.09	0.02

¹Genetic correlation are above the diagonal, environmental correlations are below the diagonal, and heritabilities are on the diagonal in bold type.

tability estimates were similar to previous estimates for this and other populations (Weller and Ezra, 1997; Kadarmideen et al., 2003). Heritability was highest for fat, and lowest for fertility. Variance components were similar for the 3 milk production traits.

The genetic and environmental correlations and heritabilities from the multitrait AM analyses are presented in Tables 4 through 8. Generally the estimates for production traits were similar to previous multiparity REML analyses (Albuquerque et al., 1996). The multitrait AM heritabilities for the individual parities were greater than the repeatability AM heritabilities, and individual parity multitrait heritabilities decreased with increase in parity number. The estimates for the early parities are probably biased downwards, because a selected sample of animals was analyzed. Only cows with valid records for all 5 lactations were included in the analyses. Similar to the repeatability AM, heritabilities were higher for production traits, lower for SCS, and lowest for fertility. Heritability was again highest for fat yield. The genetic correlations among parities were higher than the environmental correlations. Genetic correlations between parities decreased with increase in the difference in parity number, but all were greater than 0.5. The environmental correlations were higher for production traits, lower for SCS, and close to zero for fertility.

In the analyses of the complete populations, there were 508 bulls with reliabilities greater than 0.5 for the production traits. All correlations between the repeatability AM and multitrait AM index evaluations of these bulls were greater than 0.97. The correlations for fat and protein percent were nearly unity, which is not surprising, considering that the heritabilities for these traits are greater than for the milk production traits.

The single-parity protein evaluations and index values are given in Table 9 for 17 bulls with more than 5000 daughter records. All these bulls had reliabilities greater than 0.99. These bulls were divided into 3 groups, based on the cow maturing trend. There were 8 bulls for which the evaluations decreased with in-

Table 9. Genetic evaluations for protein yield of bulls with >5000 daughter records.

Sire number	Parity					Index	Type ¹
	1	2	3	4	5		
829	-1.4	-2.8	-3.8	-5.1	-5.4	-2.9	-
2122	-2.0	-7.2	-8.5	-8.4	-6.7	-5.7	-
2124	-2.4	-5.7	-5.9	-5.7	-5.0	-4.5	-
2132	0.3	-6.9	-7.2	-6.9	-5.8	-4.3	-
2154	-4.0	0.3	2.8	5.7	7.4	0.4	+
2283	3.9	-2.4	-3.9	-5.1	-6.5	-1.1	-
2303	3.4	-6.0	-7.4	-8.2	-7.9	-3.3	-
2335	-3.5	-4.6	-3.6	-1.8	-0.9	-3.4	×
2357	6.3	8.8	6.8	4.1	2.0	6.4	×
3070	5.3	6.1	7.7	8.6	8.7	6.6	+
3089	4.8	11.8	13.3	13.9	12.9	9.9	+
3099	5.6	1.4	-0.5	-2.8	-4.5	1.6	-
3212	9.5	12.3	11.9	11.2	9.4	10.9	×
3241	-5.9	-0.9	1.1	3.1	4.2	-1.4	+
3274	1.7	14.1	15.8	16.6	15.3	10.4	+
3304	11.1	10.6	9.6	8.0	5.8	9.9	-
3376	8.2	13.9	13.4	11.8	9.3	11.2	×

¹ +, Sires with evaluations that increase with parity number; -, sires with evaluation that decrease with parity number; ×, sires without a clear parity trend.

creasing parity, 5 bulls for which the evaluations increased, and 4 bulls without any clear trend. Some of the differences were quite dramatic. For example, the index values of sires 3274 and 3304 were nearly equal. However, at first parity, the evaluation of sire 3304 was nearly 10 kg higher than sire 3274, while at fifth parity the situation was reversed. Note that the evaluation of sire 3304 continued to decrease through the fifth parity.

Of these 17 bulls, 2 included in the analysis of Weller and Ezra (2001) displayed strong RIP-dip effects, 3212 and 3241. The protein evaluations of both bulls increased from first to second parity, and the evaluation of 3241 continued to increase through fifth parity. A third sire, 3148, not included in Table 10 also displayed strong RIP-dip in the analysis of Weller and Ezra (2001). His protein evaluations increase by 2.3 kg from first through third parities. These results correspond

to the hypothesis presented in the introduction that one of the causes of RIP-dip observed with the repeatability AM is bulls whose genetic value increases from first to later parities.

The annual genetic, phenotypic, and environmental trends are given in Table 10 for all traits. The phenotypic and environmental trends were positive for all traits, except for SCS and female fertility. However, increased SCS is economically unfavorable. The absolute values of the phenotypic trends were greater for all traits, except for SCS and female fertility. The genetic trends were positive for all traits, except for female fertility by the repeatability AM. All other trends were significantly different from zero at $P < 0.0001$. The small positive trend for female fertility is somewhat surprising, considering that many studies have found negative genetic correlations between milk production and fertil-

Table 10. Annual genetic, environmental, and phenotypic trends for all traits analyzed.

Trait	Trends				
	Genetic			Phenotypic ¹	Environmental ²
	Repeatability model	Multitrait model			
		First parity	Index		
Milk (kgs)	65.1	53.7	61.8	127.1	73.4
Fat (kgs)	2.23	2.00	2.35	6.35	4.35
Protein (kgs)	2.55	2.15	2.49	4.53	2.38
% fat	0.0012	0.0026	0.0035	0.0214	0.0188
% protein	0.0059	0.0052	0.0062	0.0061	0.0009
SCS	0.013	0.014	0.010	−0.091	−0.105
% female fertility	0.000	0.049	0.023	−0.178	−0.227

¹First parity.

²Phenotypic trend—first-parity genetic trend.

Figure 1. Mean breeding values of cows for the individual parity evaluations of protein yield by birth year. ····, first parity; ---, second parity; —, third parity; - - -, fourth parity; — · —, fifth parity; —, multiparity index.

Figure 3. Multiparity index mean breeding values of cows by birth year for fat and protein concentration. —, fat percentage; ····, protein percentage.

ity (summarized by Kadarmideen et al., 2003), but correspond to previous results for the Israeli Holstein population (Weller and Ezra, 1997). It is possible that natural selection compensates for the negative genetic correlation with production.

The means of breeding values for protein for the individual parities from the multitrait AM are plotted in Figure 1. The genetic trend was highest for second parity and lowest for fifth. It is not surprising that genetic trend was lowest for fifth, because nearly all selection decisions are made prior to realization of fifth-parity lactations, and heritability was lowest for this parity. The fact that genetic trend was greater for second, 2.71 kg/yr, than for first parity, 2.16 kg/yr, may be because the variance was greater for second parity even after multiplicative adjustment, and genetic correlations with the later parities were higher for second. The stan-

dard errors of these trends were both 0.0028 kg/yr. Thus these differences were highly significant. The genetic trend for fourth parity was very close to the trend for the multiparity index.

It should be noted that all the genetic trends and breeding values are somewhat effected by the (co)variance components used to compute the genetic evaluations. These were derived by the REML analysis of cows with valid records for all 5 parities. As noted previously, this sample is somewhat biased, and may have affected the evaluations obtained.

The means of cow breeding values for the multiparity index are given in Figure 2 for milk, fat, and protein yield, in Figure 3 for fat and protein percentage, and in Figure 4 for SCS and female fertility. Fat and protein production increased nearly linearly over the entire

Figure 2. Multiparity index mean breeding values of cows by birth year for production traits. — Milk; ···· fat; - - -, protein.

Figure 4. Multiparity index mean breeding values of cows by birth year for secondary traits. —, SCS; ···· female fertility.

range of birth years, while milk increase rapidly until 1991, and then remained nearly constant. This can be explained based on the evolution of the Israeli selection index. Until 1990, selection was for an index of milk and fat production. In 1990 selection was only on protein, and since 1991 selection has been chiefly for protein with a negative value for milk production. Therefore, as also shown in Figure 3, fat and protein percentage decreased until 1990, but have since increased at nearly the same rate. Even though the coefficient for protein was 5.4 times the fat coefficient for the period 1991 to 2001, these 2 traits are expected to increase at the same rate, because both the variance and heritability are higher for fat yield (Wilmink, 1987).

The genetic level of SCS increased until 1993, and since then the trend has been negative (i.e., economically positive). This result is somewhat surprising, considering that SCS was officially included in the breeding index beginning in 1996. One possibility is that there was farmer-driven selection for this trait prior to its official inclusion in the index. Female fertility was only included in the index in 2000, which should not affect the results of this study. No clear trend is evident for this trait in Figure 4. The increases and decreases in the graph are apparently due to the effect of specific widely used bulls that were either strongly positive or negative for this trait.

Several studies have proposed genetic evaluation for milk production traits and SCS by test-day models (Reents et al., 1995; Wiggans and Goddard, 1997; Schaeffer et al., 2000; Swalve 2000; Jensen, 2001). Test-day models have the advantage that they can correctly account for differing numbers of records among lactations, but require much more intensive computation. In addition, test-day models require estimation of many more parameters than lactation-based models (Misztal et al., 2000). It is not clear how inaccuracies in the estimation of these parameters affect the derived evaluations. Furthermore, the test-day model apparently does not completely solve the "RIP-dip" problem for lactations in progress (Mrode et al., 2000). The multitrait lactation model is therefore an attractive compromise between repeatability lactation models, which do not account for maturing trends across parities, and test-day models that are much more demanding computationally.

CONCLUSIONS

The multitrait heritabilities for individual parities were greater than the heritabilities from the repeatability AM, and heritabilities decreased with an increase in parity. Heritabilities and environmental correlations among parities were highest for production traits, lower for SCS, and lowest for fertility. Genetic correlations

were higher than the environmental correlations. Genetic correlations decreased with an increase in the difference in parity number, but all were greater than 0.5.

Genetic trends from the repeatability and multitrait models were very similar. The genetic trend for SCS was economically unfavorable until 1993, and since then it has been favorable. The genetic trend for female fertility was close to zero, but the annual environmental trend was -0.2% . The multitrait lactation model is an attractive compromise between repeatability lactation models, which do not account for maturing trends across parities, and test-day models that are much more demanding computationally.

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