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**Genetic Evaluation of Dairy Cattle by Multi-Trait
Methodology and Comparison of 5 National
Holsten-Friesian Breed Strains for Economic
Performance**

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C. ABSTRACT

Methodologies for genetic evaluation of bulls and cows for production traits were improved by preadjustment of records, and by accounting for heterogeneous variances among herds. Improved methods were developed for genetic evaluation of categorical traits, and to estimate variance and covariance components by restricted maximum likelihood when all traits are not recorded on all individuals.

Twenty-six elite sires from the US, Canada, New Zealand, Sweden, and Israel were compared under conditions of intensive management in Israel. Significant strain effects were found for all traits tested. Israeli sires were highest for milk and fat production, and cow survival. New Zealand sires were highest for fat percent, and most favorable for calving traits. Canadian sires were largest, and most favorable for conformation traits. Swedish sires were highest for fertility. However, the results of this experiment do not to accurately reflect genetic differences among the base populations.

Genetic parameters were estimated for health and fertility traits. A negative genetic relationship between fertility and production was found in the US, but not in Israel. Factor analysis of conformation traits demonstrated that 18 conformation traits scored in the US could be reduced into eight phenotypic and seven genetic factors. More emphasis on secondary traits, particularly fertility, could yield significant genetic gains, with only a 10% decrease in progress for milk production.

D. OBJECTIVES OF THE RESEARCH

1. To modify models for multi-trait cow and sire evaluations and to test their contribution to increasing economic return from selection.
2. To evaluate important economic characters of highly selected bulls from the five highest milk producing Holstein-Friesian strains under conditions of intensive management; and to establish the potential contribution of each strain to improve yield, yield persistency, reproduction, calving performance, conformation, and mastitis resistance over three lactations.
3. To explore the effect of inbreeding on growth, production and reproduction and to determine whether the effect is general or interacts with sire families.
4. To incorporate mastitis recordings and veterinary diagnoses in progeny testing and estimate their contribution to economic gain from selection.
5. To determine the relative weight which should be applied in selection for yield, persistency, dystocia, calf mortality, mastitis, conception and culling rates and conformation traits.

E. DESCRIPTION OF THE RESEARCH ACTIVITIES AND RESULTS

Introduction

Dr. Reuven Bar-Anan was the principal investigator of this project until his untimely demise in November, 1986. His death was a great loss to agricultural research in general, and this project in particular. The remaining investigators have done their best to continue the research as originally planned. Although we believe that this project has resulted in a major contribution to agriculture in both countries, much more could have been accomplished if Dr. Bar-Anan had remained among us.

Five objectives were defined in the proposal for this project, but as the research progressed, it was found that the investigation of inbreeding was less promising than originally thought. Mean inbreeding level in the Israeli population was low, and we were not able to define sire families appropriate for the proposed research. Since research in that direction was not pursued, the project report is divided into the results for the remaining four objectives.

Publications of this project are cited in the report by author and year. A more complete citation is presented for external references. Multiple publications by the same authors in the same year are denoted by addition of consecutive letters after the year in both citations and the publication list.

Objective 1. Genetic evaluation of sires and cows, and (co)variance
component estimation

A. Current procedures and problems in genetic evaluation of dairy cattle.

In both the US and Israel, genetic evaluation of dairy cattle is based on analysis of field data, rather than controlled experiments. The disadvantage of this approach is that the data structure is much less amenable to analysis than experimental data. Cows raised on commercial herds are grown and produce under different management systems, thus to obtain unbiased genetic evaluations it is necessary to correct for the effect of herds, years, and calving seasons. To obtain sufficient number of records to estimate herd-year-season (HYS) effects, and to obtain sire evaluations based on all of a sire's daughters, genetic evaluations are computed using all available records over a period of years. Furthermore, due to rapid genetic improvement of dairy cattle during the last 30 years, neither cows nor sires from different periods can be considered a random sample from the same genetic population.

Since 1960, genetic evaluations have been calculated by mixed linear models, where the genetic effects are considered random, and HYS effects fixed. Genetic evaluations derived from these models are Best Linear Unbiased Predictions (BLUP) of the true genetic values. All mixed models require accurate estimates of the variance components

of the random effects. Traditionally the sire model was employed, in which a sire's daughters are considered repeat samples of the sire's genetic value.

Until the middle of the last decade, genetic trend was accounted for by grouping sires by age. In 1976, Henderson developed an algorithm to invert the numerator relationship matrix. This matrix can then be incorporated into the mixed model equations used to compute genetic evaluations, accounting more accurately for genetic trend and relationships between animals. During the last few years, the animal model has come into use, in which each animal is considered a separate effect. Genetic relationships among animals are accounted by the inverse of the numerator relationship matrix.

The first objective of this project was to investigate methods to improve genetic evaluation of animals, by preadjustment of records, more accurate estimation of variance components, and more efficient computer algorithms.

B. Improving sire and cow evaluation by pre-adjustment of records.

To maximize genetic progress, environmental influences that limit the accuracy of selection should be eliminated. Methods were developed in both countries to adjust production records for each cow's previous reproductive history. In Israel, adjustment factors were estimated by Ezra, Weller, and Bar-Anan (1986) for calving age and month. Factors to extend partial lactations were developed by

Bar-Anan, Weller, Wiggans, and Osterkorn (1986). Weller (1988) developed a method to differentially weight lactations in progress in the computation of genetic evaluations, that is only slightly more complicated than procedures currently in use.

Weller, Bar-Anan, and Osterkorn (1985) derived correction factors for days open for annualized yield $[365(\text{total lactation yield/calving interval})]$ of Israeli Holsteins by smoothed least square means of days open classes. Additive adjustment factors were more appropriate than multiplicative adjustment factors. Records adjusted for days open were not able to predict the following lactation yield significantly better than unadjusted records. The optimum open period length was greater for primiparous, than for multiparous cows. Yield was maximum with more days open for cows with low peak production. Conception prior to 2 mo postpartum had an adverse effect on cumulative yield.

The effect of adjusting US production records for present days open, previous days open, and previous days dry were determined by Funk, Freeman, and Berger (1987), Sadek, Freeman, and Berger (1988), and Sadek (1988). Three analysis models were compared. The first two models evaluated Holstein young bulls for production using first lactations of their first crop daughters and their herdmates with and without adjusting records for days open. Effect included in the first model were the mean, HYS, groups, sires of herdmates and young bulls within groups. Young bulls were considered random and sires of herdmates were considered fixed. In the second model, the same effects were used, considering all bulls and sires random. The

inverse of the relationship matrix among bulls, their sires and maternal grandsires was included in all models. Data were 24,997 progenies of 484 young bulls and 119,013 herdmatres progenies of 291 sires, both distributed over 16,015 HYS. The maximum differences among adjusted and unadjusted young bulls' predictors were 303 kg of milk and 9.4 kg of fat, for the first model, and 280 kg of milk and 8.6 kg of fat, for the second model. The rank correlations among adjusted and unadjusted bulls' predictors were 0.99 for milk and fat, using the first model, and 0.98 for milk and fat, using the second model. However, the rank correlations for the top 5% of the young bulls were 0.84 for milk and 0.92 for fat by the first model, and 0.75 for milk and .82 for fat by the second model. For the bottom 5% of the young bulls the rank correlations were 0.76 for milk and 0.91 for fat by the first model, and 0.82 for milk and 0.91 for fat by the second model.

In the third model, sires and cows were evaluated for production using multiple lactations records with and without adjustment for present days open, previous days open, and previous days dry. This model included the mean, HYS, groups, sires within groups, and cows nested within sires. This model was used to analyse 678,502 lactations of 315,502 cows, daughters of 522 sires distributed over 97,804 HYS. These data included 281 dams of 308 young bulls. The maximum differences among adjusted and unadjusted sires' predictors were 228 kg of milk and 7.2 kg of fat. Among dams' predictors, the maximum differences were 1118 kg of milk and 41 kg of fat. The rank

correlations among adjusted and unadjusted sires' predictors were 0.99 for milk and fat. Among adjusted and unadjusted bull dams' predictors, the rank correlations were 0.95 for milk and 0.97 for fat. However, the rank correlations for the highest 5% of sires were only 0.77 for milk and 0.91 for fat. For the lowest 5% of sires, the rank correlations were 0.94 for milk and 0.95 for fat. Rank correlations were 0.7 for milk and 0.59 for fat of the top 20 dams and 0.85 for milk and 0.72 for fat of the bottom 20 dams.

Pedigree indices for young bulls were calculated using various combinations of sire, dam, and maternal grandsire and information on past reproductive performance of the ancestors. Adjusting pedigree information for past reproductive performance improved the prediction for sires and maternal grandsires in predicting young bulls' proofs. However, the regression coefficients for dams were much smaller than the theoretically expected coefficients with or without adjustment. Adjustment gave no real improvement for dam's as predictors of son's progeny tests. We recommend that lactation records used for genetic evaluation should be adjusted for days open.

C. Methodologies for cow evaluation.

There are three main goals in cow evaluations, selection of superior cows to be used as bull dams, selection of cows to serve as embryo donors, and identification of inferior cows to be culled from the population. Preliminary results indicate that under Israeli

conditions, criteria for selection for these goals are not identical.

In most advanced breeding programs, bull dams are selected based on their genetic evaluations for production and conformation traits. In Israel selection of bull dams based only on genetic evaluations may lead to a significant increase in inbreeding and reduction of the genetic base of the population. This is because in the relatively small Israeli population, most cows with the highest genetic evaluations will be daughters of only a few bulls. It is therefore suggested that selection of bull dams be based on an index of the cows' genetic and phenotypic evaluations for production and conformation traits.

A method for more accurate genetic cow evaluations was developed by Weller, Wiggans and Lawlor (1987). This method computes cow evaluations as back solutions from the sire evaluations, but includes the genetic level of the dam in the final cow evaluations. The method was tested on the complete Israeli population, by comparing bull dam evaluations to their sons' genetic evaluations. Correlations were near the expected values based on the dam and son repeatabilities.

D. Heterogenous within herd variances.

A number of studies have found previously that sire and residual variance components, and heritability increase with herd production level. Weller, Ron, and Bar-Anan (1987) stratified herd-years of Israeli-Holsteins into three groups by two criteria: 1) mean annual

milk production, and 2) mean persistency, estimated as the ratio of daily milk production at the 5th mo postpartum to daily production during the postpartum peak period. As found in previous studies, both sire and residual variance components, as estimated by Henderson's method 3, and heritability increased with increased production level. This was true for both primi- and multiparous cows, but the effect was greater for multiparous cows. Even though production and persistency were correlated, no clear trends were evident for stratification by persistency; thus a relationship between stress and heritability was not established. Genetic correlations among stratification groups were between .7 and .9 for persistency, and between .6 and .86 for production. The lower correlations for production are indicative of a greater sire x environmental interaction for production levels.

Boldman and Freeman (1988), and Boldman (1988) estimated variance components for the US population by restricted maximum likelihood (REML) for milk yield and log yield at three production levels. The model of analysis included fixed HYS and genetic group effects in addition to random sire, cow nested within sire, and residual effects. Additive genetic relationships among sires were included. Additive genetic variance (AG) was estimated as four times sire variance. Permanent environmental variance (PE) was estimated as cow variance minus three times sire variance. Data were 121,136 305 day mature equivalent (ME) first and later lactation yields for 91,206 cows calving between 1979 and 1984 throughout the US. 526 sires were represented and 485 of these had first crop daughters in the data.

Production levels were defined on the basis of mean ME milk yield of all cows freshening in the same herd-year, regardless of whether the record was included in the analysis or not. Upper and lower limits used to define production levels were: low, 5897-7484 kg; medium, 7485-8618 kg; and high, 8619-10,206 kg.

Estimated variance components for untransformed and log transformed milk yield at the three production levels are in Table 1. Estimates of heritability and repeatability are given in Table 2. Estimates for each variance component increased with production level for untransformed yield. AG increased at the greatest relative rate, doubling from the low to high production level. Increase in AG with mean yield was smaller for log yield than untransformed yield. For log transformed yield, PE and residual variance (RES) decreased as production level increased, resulting in repeatabilities that were slightly less for low average yield herds, and similar for medium and high herds. Log transformation did not change heritability and repeatability estimates.

Table 1. Estimated variance components of untransformed and log transformed milk yield by level of production.

Level of production	Variance components					
	Untransformed yield [(kg) ²]			Log yield [(1000 kg) ²]		
	AG	PE	RES	AG	PE	RES
Low	258,203	483,789	731,731	5539	11,006	17,658
Medium	386,705	550,655	805,389	6176	9504	14,087
High	510,055	634,780	958,277	6490	8728	12,770

Table 2. Estimated heritability (h^2) and repeatability (rpt) of untransformed and log transformed milk yield by level of production.

Level of production	Untransformed yield		Log yield	
	h^2	rpt	h^2	rpt
Low	.18	.50	.16	.48
Medium	.22	.54	.21	.53
High	.24	.54	.23	.54

Weller, Ron, and Bar-Anan (1985) developed an algorithm to compute mixed-model evaluations with the variance components computed as functions of an environmental gradient. A genetic correlation of unity is assumed. Prior to the construction of the mixed model equations, the square root of the sire component of variance is computed for each herd-year-parity group as a linear or quadratic function of the mean herd-year-parity level. Each record is then divided by the square root of its sire component of variance to obtain equal sire components of variance for all records. The resultant residual variances are then computed for each herd-year-parity group as a function of its production level. The inverse of these values are used to weight the contribution of each record in the construction of the mixed model equations. The correlation between evaluations obtained assuming equal variance components, and herd-year-parity level dependent variance components was .99, but the mean repeatability of the latter were 2% higher.

Boldman (1988) computed genetic evaluations of US sires and cows with three models. In the first model, variance estimates for untransformed (linear) yield at the medium production level were used

for all records. In the second model, yield was transformed to the natural logarithm scale, and variance estimates from the medium level were used. In the third model, untransformed yield was used and heterogeneous variances at the three production levels were accounted for by a method similar to Weller, Ron, and Bar-Anan (1985), which was proposed independently by Gianola in 1986. In this procedure, genetic variance was standardized by dividing each record by the genetic standard deviation corresponding to the level of herd production. Permanent environmental and residual variance matrices, heterogeneous by production level, were then used in the mixed model equations. Each model included fixed HYS and genetic group effects in addition to random sire and cow nested within sire, permanent environmental, and residual effects. Relationships among sires were included in the analysis, but not relationships among mates of sires and among cows. This model was equivalent to the sire and nested cow model used for variance component estimation, but allowed heterogeneous variances to be more easily incorporated.

Rank correlations of all evaluations from the three models were greater than .99 for both sires and cows. A comparison of animal ranks from the model adjusted for heterogeneous variances with animal ranks from the unadjusted linear and log yield models is in Table 3. Sire ranks differed less than cow ranks across the three models. The smaller rank change between the adjusted model and the unadjusted linear yield model as compared to the adjusted model and the

unadjusted log yield model indicates that log transformation is inferior to simply ignoring heterogeneous variances.

Table 3. Comparison of animal ranks from the model adjusted for heterogeneous variances with animal ranks from the unadjusted linear and log yield models.

	Models compared	
	Adjusted vs. unadjusted linear yield	Adjusted vs. unadjusted log yield
Top 5% sires (n=26)		
No. in common	23 (88%)	23 (88%)
Average rank difference	1.4	2.9
Top 1% cows (n=910)		
No. in common	872 (96%)	781 (86%)
Average rank difference	48.6	185.3

Table 4 lists the number of elite cows by production level for the three models. Elite cows were the top 2% of all cows in the analysis. For all models, the greatest percentage of elite cows was found at the high production level. Compared to the unadjusted linear yield model, the unadjusted log yield model and adjusted variance model increased the percentage of elite cows in low and medium production herds and decreased the percentage in high herds. Changes in percentages of elite cows by production level were much greater for the log yield model. Use of a log yield model may result in overevaluation of cows in low production herds and underevaluation of cows in high herds, the opposite of the unadjusted linear yield model.

A model adjusted for heterogeneous variances appears to be better than log transformation and is computationally feasible if variance estimates are available. A method similar to that described by Boldman and Freeman (1988), except that the choice of categories for herd production levels be based on herd-year phenotypic variances, is recommended to be incorporated in the US animal model for dairy sire and cow evaluation. The necessary parameters will be estimated from the national data.

Table 4. Number and percentage of elite cows by production level for the three models.

Level of production	Model of analysis		
	Linear, unadjusted	Log, unadjusted	Linear, adjusted
Low	102 (0.54%)	164 (0.87%)	107 (0.57%)
Medium	386 (0.90%)	429 (1.00%)	419 (0.97%)
High	422 (1.45%)	317 (1.09%)	384 (1.32%)

E. Iterative algorithms for solving mixed model equations.

Berger, Luecke, and Hoekstra (1987, 1989) investigated algorithms for iterative solutions to mixed model equations. Successive-overrelaxation with adaptive acceleration and a Jacobi conjugate gradient method seems to be more generally useful for two general areas of interest: 1) sire evaluation models, where some effects are absorbed; and 2) reduced animal models, where no effects are absorbed. All algorithms converged with the inverse of relationships as part of

the information matrix. Key features include: 1) scaling the equations so that all diagonal elements are one and the scaled coefficient matrix remains real, symmetric, and positive definite; 2) calculation of the relaxation parameter during run time to approximate the value that will yield fastest convergence; 3) calculation of a new relaxation parameter after convergence begins to slow down; and 4) use of numerically accurate and efficient convergence criteria. Jacobi conjugate gradient and successive overrelaxation were compared with other methods on a set of reduced animal model equations of order 3356. Number of iterations and execution times were: 40, .38 sec and 37, .40 sec, respectively. Another application of order 38,139 took 38 CPU sec (50 iterations). A sire evaluation model of order 9,711 converged after 152 iterations. Successive-overrelaxation with adaptive acceleration and use of a Jacobi conjugate gradient is an efficient way to compute sire solutions for models useful in animal breeding.

F. Estimation of variance and covariance components.

During the first two years of the project, a general-purpose program was written by the US investigators to compute REML estimates of variance and covariance components for several models commonly used by animal breeders (Van Randen, 1986; Van Raden and Freeman, 1986; Van Randen and Jung, 1988). All traits must be recorded on all animals. This program utilizes several new computing strategies to reduce

costs. It outputs heritabilities, genetic and residual correlations, and transmitting abilities of sires computed as if estimated variances and covariances are true values. The program was made available to the Israeli investigators and is available to other researchers upon request.

Valente (1988) upgraded this program to handle the situation where all traits are not recorded on all animals. Valente and Berger (1988) used this program to analyze US dairy cattle production and fertility data. Estimates were obtained by two forms of the expectation maximization algorithm (EM1 and EM2) and a third shortcut algorithm (SHC), which uses EM for the within sire component and the "method of scoring" for the between sire component. SHC was more efficient than either EM1 or EM2. The analysis of the complete data set by SHC converged after 6 iterates, while EM1 and EM2 required 42 iterates to satisfy the same convergence criteria. In the equal data, no missing trait case EM1, EM2 and SHC required 31, 45, and 6 iterates respectively. The advantage of SHC over EM1 and EM2 were demonstrated by additional analyses of simulated data.

Estimates of covariance components can be readily derived from estimates of variance components using the equation of Searle and Rounsaville (1974, Am. Statist. 28:67), if all traits are recorded on all individuals. Weller and Ron (1987) demonstrated that estimates of covariance components by this equation can be unreliable if all traits are not recorded on all individuals, even if only a small fraction of the records are missing, and the missing records are a random sample

of the population. This problem can be solved, provided that the missing records are a random sample, by deletion from the analysis of individuals recorded for only one trait of each pair. If individuals with missing records are not a random sample, then estimates derived by this procedure will be biased.

Objective 2. Evaluation of genetic resources

A. Comparison in Israel of elite sires from five improved Holstein strains.

Dairy cattle breeders in countries with high yielding strains are confronted with the choice of whether to select within the national strain or to utilize progress in other countries by importing genetic material. In the FAO Holstein-Friesian breed comparison, strains from ten countries were compared in Poland by inseminating Polish Friesian cows with semen from young, unproven, sires from ten countries. The mean yield of the F-1 daughters under conditions of extensive management was 3615 kg milk in 305 days (Stolzman et al., World Anim. Rev., 38:9, 1981) and under more intensive conditions 4970 kg milk (Jasiorowski et al., Livest. Prod. Sci., 10:109, 1983; Stolzman et al., World Anim. Rev., 41:46, 1982). The differences among strains found in this study may not be applicable to conditions of intensive management due to genotype x environment interaction.

The Holstein-Friesian proven sire comparison in Israel was planned to compare high yield proven sires under conditions of intensive management, from the five national Friesian strains with the highest 305-day milk production in the Polish experiment: United States (US), 4183 kg; Israel (IS), 4102 kg; New Zealand (NZ), 4023 kg; Canada (CA), 3984 kg; and Sweden (SW), 3865 kg (Stolzman et al., World Anim. Rev. 38:9, 1981). High repeatability evaluations of the same sires in different countries are necessary in order to estimate genotype x environment interaction, and to compare different sire evaluation schemes. Complete results of this experiment were presented by Bar-Anan, Heiman, Ron, and Weller (1987).

The national AI organizations of CA, NZ, SW and IS selected five high milk yield proven sires each. In the US, one sire was selected from each of four US studs and two half-brothers of similar merit (Le-Del and Shade), were selected from a fifth US stud. Most sires were considered elite in the countries of origin at the start of the experiment. The sire names, identification numbers, evaluations (EVA) for milk and fat, and repeatabilities (RPT) in the countries of origin are listed in Table 5.

All available RPT values were $\geq .95$. The underlined part of the sire names are used to identify the sires. EVA for US, Swedish, and Israeli sires are in kg predicted difference. Canadian EVA were converted from BCA values by multiplication by 55 for milk and fat, respectively. EVA of New Zealand sires are in breed indices. EVA for fat and RPT values were not available for the Swedish sires.

Table 5. Sire Evaluations (EVA) and Repeatabilities (RPT) in the country of origin.

Strain	Sire	ID number	EVA		RPT
			milk	fat	
United States	I.O. State Chief <u>FORD</u>	1674245	602	13	0.99
	Arlinda Jet <u>STREAM</u>	1558842	468	6	0.99
	Butterday Burke- <u>ADMIRAL</u>	1662606	79	10	0.99
	Ideal Superior <u>LE-DEL</u>	1647190	244	-3	0.99
	Abner Ideal <u>SHADE</u> Acres	1692687	292	1	0.99
	Poly-Royal <u>DAN-VER</u>	1613259	190	14	0.99
Canada	Roybrook <u>STARLITE</u>	308691	440	24	0.99
	Clinton <u>CAMP</u> Majesty	333473	440	6	0.99
	Puget Sound <u>SHEIK</u>	327279	55	26	0.99
	Almerson Rockman <u>LESTER</u>	320022	110	10	0.99
	Rolling Lawns <u>BRENT</u>	329511	275	4	0.99
New Zealand	Graham Jimmy <u>SHAMROCK</u>	44903	118	135	0.99
	Lombard <u>BLAIR</u>	57784	123	130	0.95
	A.B. Monarch <u>ASHTON</u>	57924	127	142	0.94
	Jeeves <u>MAHANA</u>	56903	117	132	0.95
	Aupouri Sticky <u>MIKE</u>	57948	113	129	0.95
Sweden	<u>SLASS</u>	34454	406		
	<u>FRANKT</u>	33834	416		
	<u>FEX</u>	34209	472		
	<u>AMIRZ</u>	34416	385		
	<u>LIFT</u>	35365	509		
Israel	<u>CHASHMAN</u>	695	326	6	0.99
	<u>SHAFAN</u>	781	487	10	0.99
	<u>PIRCHACH</u>	783	608	16	0.99
	<u>AMIR</u>	787	428	6	0.99
	<u>GYUS</u>	829	873	18	0.99

The experiment was planned to achieve an orthogonal design of sires and strains across herds. 400 semen doses were provided for each sire except Le-Del and Shade, for which 200 doses were provided. The design of the experiment and the realised frequencies at each step are given in Table 6. Only nulliparous heifers were inseminated. All

progeny were raised on Kibbutz (communal) herds. Mean herd size was 300 cows.

Table 6. Designed and realized structure of the experiment.

	Design (n)	Realized (n)
Strains	5	5
Sires	25	26
Herds	100	111
Inseminations	10000	9411
Inseminations/strain	2000	1763 - 2067
Calvings	5000	4914
Daughters	2000	1483

The time table of the experiment is given in Table 7. F-1 heifers were first inseminated with semen from Israeli proven sires at about 14 months of age. Mean age at first calving was 2 years. A typical daily ration during lactation was 20 kg dry matter, of which 70% was concentrates. Forage consisted of corn silage, wheat silage, and hay. Crude protein content of the dry matter was ~16%. Cows were milked three times daily. Inseminations of F-1 cows began 60 days after parturition.

Genetic evaluations for all traits except body weight and percent fat were computed by mixed model methodology. The means of the traits analyzed are listed in Table 8. Only primiparous cows were analyzed for difficult calvings (DIFF), calf mortality (MORT), culling rate (CULL), and conformation traits. DIFF was scored as 100 if birth was difficult, and 0 otherwise. MORT was scored as 100 if the calf died

within 2 days of birth and 0 otherwise. Means for calving difficulty and calf mortality are as sire of calf. Scoring for conformation was on a scale of 1 to 5. Scoring for body size was from smallest to largest. Scoring for the other conformation traits was from least to most favorable. Since conformation traits are in standardized units, the means are not listed. Conception (CONC) was determined by veterinary examination after insemination. CONC was scored as 100 if the cow conceived and 0 otherwise. Inseminations of nulliparous heifers were not included in the analysis. CULL was scored as 100 if the cow was culled due to infertility, low production or mastitis, and 0 otherwise. The analysis for CULL included cows with first calving at least one year prior to the date of analysis. Means for production traits are expressed as 36-month calving equivalent. Variance components are not listed for body weight and percent fat because body weight was evaluated by a fixed model, and evaluations for percent fat were derived from those of kg milk and kg fat.

Table 7. Time scale of the experiment.

Stage	Beginning	End
Inseminations of mates	May 1981	Sept. 1982
Calvings of mates	Feb. 1982	May 1983
First calving of daughters	Dec. 1983	July 1985
Weighing of cows and scoring for conformation traits	July 1984	Dec. 1985
Data analysis	July 1986	Sept. 1986

Table 8. Means and variance components for the traits analyzed as percent of the total variance.

Analysis	Means	Variance components			
		Sire of calf	Sire of cow	Cow	Residual
Calving difficulty (%)	13.20	1.3	.9	-	97.8
Calf mortality (%)	11.00	.5	.8	-	98.6
Body size	-	-	3.5	-	96.5
Dairy character	-	-	2.0	-	98.0
Front udder	-	-	15.6	-	84.4
Rear udder	-	-	9.3	-	90.7
Teat placement	-	-	5.7	-	94.3
Conception rate (%)	48.30	-	.5	-	99.5
Culling rate (%)	20.70	-	2.5	-	97.5
Milk (kg)	8825.00	-	5.0	45.0	50.0
Fat (kg)	287.00	-	5.0	45.0	50.0
Percent fat	3.34	-	-	-	-
Body weight (kg)	480.00	-	-	-	-

Annualized yields for kg milk and fat were adjusted for days open, month and age of calving, and parity (Ezra, Weller, and Bar-Anan, 1986; Weller, Bar-Anan, and Osterkorn, 1985). The base for adjustment was March calvings of second parity cows, at 36 months of age, and 90 days open. Partial records were extended as described by Bar-Anan, Weller, Wiggans, and Osterkorn (1986). Records were deleted if i) sire, cow, herd, parity, birth date, or calving date was unknown; ii) days in milk was less than 34 or there were fewer than two valid monthly tests; and iii) if the first parity record was invalid or missing. Persistency (PERS) was computed as: [fat yield between calvings]/[365(peak yield)]. Peak yield was defined as the mean of the highest two daily fat yields prior to 90 days post partum.

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PERS was computed only on complete lactation records. Sire means were computed for all traits. Strain means were computed as mean of sire means.

Variance components for calving and conformation traits were estimated by Henderson's method III. Variance components currently used in Israel for standard sire evaluations were used for the other traits. Means and variance components of the traits analysed as fractions of the total variance are listed in Table 8.

The model of Weller, Ezra, and Bar-Anan (1986) was used for calving traits. The repeatability model was used for analysis of milk and fat, and a sire model was used for CULL and conformation traits. Sires were assumed to be unrelated in all analyses. PD's for all traits were computed as the sum of the group and sire effects. RPT was computed as follows:

$$RPT = 1 - D_j(\text{Var } e/\text{Var } S)$$

Where $\text{Var } e/\text{Var } S$ is the ratio of residual to sire variance and D_j is the diagonal element of the inverse of the coefficient matrix for the j -th sire. For evaluations from the repeatability model, D_j was estimated as the reciprocal of the diagonal element of the coefficient matrix for the j -th sire.

The following model was used for analysis of body weight:

$$Y_{ijkl} = G_i + S_{ij} + \text{PAR}_k + a(\text{DIM}) + b(\text{DIM})^2 + c(\text{AGE}) + e_{ijkl}$$

where Y_{ijkl} is the weight of the l -th cow, in the k -th parity, daughter of the j -th sire, of the i -th strain; G_i is the effect of the i -th strain, S_{ij} is the effect of the j -th sire of the i -th strain; PAR_k is the effect of the k -th parity, either one or two; DIM is days

in milk at time of weighing; AGE is the cow's age in days at weighing; a, b, and c are regression coefficients; and the other terms are as defined previously. All effects were assumed fixed, and the least square means were computed for strain and sire effects.

The analyses for calving traits, CULL, milk, and fat were performed on the entire edited Israeli Holstein-Friesian population, in order to obtain more accurate estimates of levels of effects with low frequencies in the experimental sample, HVS effects in particular. Genetic and environmental parameters for production and calving traits in the general population are summarized in Weller (1988b). Means of the general population for production traits in 1984 were 8816 kg milk, 280 kg fat, and 3.24% fat. As stated previously, CULL and calving traits were analyzed only on primiparous records. The means in the general population of primiparous cows for these traits were 16.4% CULL, 8.5% DIFF and, 7.4% MORT. Israeli sires of the general population were grouped biennially by year of birth. Records of parities greater than three were not included. The analyses for milk, fat, and CULL included all valid records since 1976. The analyses for calving traits included all valid records since 1980. Records were deleted from the analyses for calving traits if there were fewer than 50 records for either the sire of the cow or the sire of the calf. Records were deleted from the analyses for milk and fat if there were fewer than 20 valid first parity records for a sire.

PD for fat percent was computed as: $100(\text{mean kg fat} + \text{PD kg fat})/(\text{mean kg milk} + \text{PD kg milk})$, where mean kg fat and mean kg milk

are the mean kg fat and kg milk annualized yields computed from the complete population.

Genotype x environment interaction for milk production was estimated by the within-strain correlation between PD's in Israel and each of the countries of origin. Correlations were computed for each strain separately. Significance of correlations was tested against the hypothesis of zero correlation, and against the expected correlation, assuming no genotype x environment interaction. The latter is equivalent to a genetic correlation of unity, assuming milk production in Israel and the country of origin to be two different traits. The expected product-moment correlation was computed by the equation of Calo et al. (J. Anim. Sci., 37:676, 1973):

$$E(r) = \sum(RPT_{1i} \cdot RPT_{2i}) / (\sum RPT_{1i} \cdot \sum RPT_{2i})^{0.5}$$

where $E(r)$ is the expected correlation assuming a genetic correlation of unity, RPT_{1i} and RPT_{2i} are RPT for sire i in Israel and the country of origin, respectively.

Sire and strain means and PD's for DIFF and MORT are listed in Table 9. RPT for calving traits ranged from 49 to 59% as sire of the calf, and from 27 to 34% as sire of the cow. NZ was most favorable for DIFF and MORT as sire of calf, and SW was least favorable. IS was most favorable for these traits as sire of cow, and CA was least favorable. Even though these traits are known to have low heritability, and were regressed to the mean due to the relatively low number of calvings per sire, the ranges of PD's for DIFF were about 12% and 9% as sire of the calf and of the cow, respectively.

Table 9. Sire and strain means (X) and predicted differences (PD) for difficult calving (DIFF) and calf mortality (MORT) of first parity cows.

Strain	Sire	Sire of calf					Sire of cow				
		No. of calvings	DIFF		MORT		No. of dau.	DIFF		MORT	
			X	PD	X	PD		X	PD	X	PD
U.S.	FORD	192	13.5	2.1	10.4	1.3	70	8.6	.4	2.9	-2.6
	STREAM	121	15.7	3.7	9.9	1.1	-	-	-	-	-
	ADMIRAL	204	14.2	3.2	9.3	.9	76	7.9	.0	6.5	-1.4
	LE-DEL	106	6.6	-1.3	5.7	-.4	-	-	-	-	-
	SHADE	111	18.0	5.2	17.1	4.0	-	-	-	-	-0
	DAN-VER	194	16.0	4.0	13.9	3.1	75	6.6	-.7	5.3	-2.0
	X	928	14.0	2.8	11.0	2.0	221	7.7	-.1	4.9	-2.8
Canada	STARLITE	141	12.8	2.1	12.7	3.5	52	7.7	1.8	11.5	3.3
	CAMP	132	17.4	5.4	13.6	4.0	50	20.0	6.1	16.0	5.3
	SHEIK	198	13.6	2.5	13.6	3.9	74	8.1	2.0	9.5	3.5
	LESTER	201	13.9	2.9	12.4	3.4	81	6.2	1.3	8.6	3.1
	BRENT	164	15.2	3.7	12.2	3.1	49	16.3	4.9	10.2	3.7
	X	836	14.6	3.3	12.9	3.6	306	11.7	3.2	11.2	3.9
N.Z.	SHAMROCK	165	13.3	.3	10.3	-.1	61	11.5	3.2	11.5	2.9
	BLAIR	197	7.1	-3.7	7.1	-1.6	66	7.6	1.7	7.6	1.5
	ASHTON	149	6.7	-4.0	8.7	-.8	60	8.3	2.5	3.3	0.4
	MAHANA	168	10.7	-1.5	8.9	-.8	52	15.4	4.3	15.4	3.8
	MIKE	194	6.7	-3.9	8.2	-.9	83	9.6	2.5	7.2	1.3
	X	873	8.9	-2.6	8.6	-.8	322	10.5	2.8	9.0	2.0
Sweden	SLASS	143	12.6	2.4	11.2	2.8	-	-	-	-	-
	FRANKT	190	15.2	4.3	13.2	3.9	68	4.4	.0	2.9	-0.7
	FEX	229	18.7	6.9	13.9	4.4	88	3.4	-.8	2.3	-1.3
	AMIRZ	202	18.3	6.6	14.3	4.6	71	14.1	3.8	11.3	2.2
	LIFT	225	20.4	7.9	15.6	5.2	78	16.7	5.1	14.1	3.4
	X	989	17.0	5.6	13.6	4.2	305	9.6	2.0	7.6	0.9
Israel	CHASHMAN	196	11.2	.4	8.7	-.4	65	7.7	-.9	1.5	-3.5
	SHAFAN	191	5.8	-3.9	6.3	-1.7	65	3.1	-2.8	4.6	-2.3
	PIRCHACH	210	15.2	3.3	11.0	1.0	75	10.7	.4	14.7	1.5
	AMIR	210	11.0	.1	9.5	.1	76	6.6	-1.1	1.3	-3.4
	GYUS	210	14.3	2.4	9.0	-.2	75	4.0	-2.3	1.3	-3.5
	X	1017	11.5	.5	8.9	-.2	356	6.4	-1.3	4.7	-2.2

PD's for conformation traits and least square means for body weight are listed in Table 10. Standard errors of least square means ranged from 15 to 23 kg. Daughters of CA sires were heaviest, and daughters of NZ sires were lightest. The ranges of sire and strain least square means were 94 and 41 kg, respectively. The three intermediate strains were nearly identical. The ranking of the strains for appraisal of body size was similar, except that rankings for SW and IS were reversed. CA was most favorable for all conformation traits, except dairy character, for which IS was most favorable. SW was least favorable for all conformation traits.

PD's for CONC and CULL are listed in Table 11. The number of daughters for CONC is less than the number for CULL, because not all cows were inseminated. The range of RPT for CONC was 31 to 45%. The ranking of the strains from highest to lowest CONC was SW, IS, NZ, CA, and US. The ranges of PD's and strain effects for CONC were 11.7 and 7.5%, respectively. RPT for CULL ranged from 51 to 62%. CULL was lowest for IS and highest for NZ daughters. The ranges of PD's and strain effects were 24.6 and 17.5%, respectively.

Sire and strain means for persistency and days in milk during first lactation are listed in Table 12. Also listed are sire and strain means and PD's for production traits. Days in milk for IS and US daughters was about 15 days more than CA and SW daughters, and about 30 days more than NZ daughters. The ranges of sire and strain means were 62 and 36 days, respectively. NZ daughters had slightly lower persistency than the other strains, which were nearly identical.

Table 10. Sire and strain least squares means (LSM) for kg body weight, and predicted differences for conformation traits.

Strain	Sire	Body weight		Number of cows	Conformation traits				
		No. of cows	LSM		Predicted differences				Teat placement
					Body size	Dairy character	Udder front rear		
U.S.	FORD	18	464	46	.8	.5	1.5	1.7	- .7
	STREAM	14	469	29	.6	.8	- .1	.1	- .5
	ADMIRAL	25	466	41	.0	.4	.7	.4	.0
	LE-DEL	12	511	16	.7	.4	.6	1.4	.6
	SHADE	8	453	22	.5	.4	-2.1	-1.1	- .4
	DAN-VER	24	509	42	.7	.4	-1.3	- .1	-1.1
	X	101	479	196	.5	.5	- .1	.4	- .3
Canada	STARLITE	6	499	31	1.0	.6	- .5	- .1	- .8
	CAMP	12	523	29	1.4	.0	.9	.2	1.3
	SHEIK	22	488	32	.8	.1	.1	.7	.3
	LESTER	27	533	39	.8	- .3	.6	.7	1.6
	BRENT	13	475	31	.4	.1	1.6	2.0	1.6
	X	80	504	162	.9	.1	.5	.7	.8
N.Z.	SHAMROCK	11	466	28	-1.8	-1.1	1.0	.4	.6
	BLAIR	25	462	30	-1.5	- .7	.6	.1	.0
	ASHTON	16	463	32	-2.3	-1.1	.8	.3	1.0
	MAHANA	16	481	23	-1.1	- .7	- .3	.0	-1.0
	MIKE	22	439	46	-1.7	- .9	.2	- .4	.5
	X	90	462	159	-1.7	- .9	.5	.1	.2
Sweden	SLASS	11	464	19	- .6	-1.2	- .7	-1.2	-1.3
	FRANKT	18	481	43	- .5	-1.4	- .8	-1.1	-1.8
	FEX	24	483	43	- .7	-1.1	- .9	- .8	-1.6
	AMIRZ	16	479	43	- .3	-1.3	- .7	- .8	- .4
	LIFT	20	498	40	- .3	-1.4	.1	.0	- .1
	X	89	481	188	- .5	-1.3	- .6	- .8	-1.0
Israel	CHASHMAN	9	486	23	.7	1.3	.0	- .8	.8
	SHAFAN	16	467	21	.4	1.3	-2.4	-2.8	- .7
	PIRCHACH	21	480	29	.7	1.5	.7	.1	.8
	AMIR	17	448	27	.7	1.5	.7	.5	1.5
	GYUS	13	500	29	.7	1.7	- .2	.6	- .1
	X	76	476	129	.6	1.5	- .2	- .5	.5

Table 11. Sire and strain means (X) and predicted differences (PD) for conception and culling rates of first parity cows.

Strain	Sire	Conception rate				Culling rate		
		No. of		$\bar{X}$	PD	No. of		PD
		daus.	insem.			daus.	$\bar{X}$	
U.S.	FORD	63	195	43.1	-5.1	71	18.3	-3.1
	STREAM	41	122	39.3	-6.4	45	24.4	0.3
	ADMIRAL	68	197	49.7	-1.7	73	12.3	-5.6
	LE-DEL	32	90	50.0	-2.0	36	13.9	-4.1
	SHADE	39	124	39.5	-4.8	41	7.3	-8.8
	DAN-VER	73	185	41.1	-5.1	78	15.4	-4.4
	X	316	913	43.8	-4.2	344	15.3	-4.3
Canada	STARLITE	41	136	45.6	-1.7	50	12.0	-7.0
	CAMP	39	115	48.7	-1.7	47	23.4	2.6
	SHEIK	59	152	44.1	-3.6	72	34.7	9.8
	LESTER	70	175	45.1	-3.3	82	25.6	4.7
	BRENT	45	122	50.8	-.4	49	12.2	-3.8
	X	254	700	46.9	-2.1	300	21.6	1.3
N.Z.	SHAMROCK	50	110	53.6	2.4	60	33.3	12.5
	BLAIR	55	144	43.7	-2.0	64	35.9	13.4
	ASHTON	58	124	48.4	.9	60	35.0	13.0
	MAHANA	43	101	50.5	1.1	51	27.5	6.9
	MIKE	67	120	59.2	4.1	80	33.7	12.0
	X	273	599	51.1	1.3	315	33.1	11.6
Sweden	SLASS	42	113	43.4	.2	47	27.7	4.5
	FRANKT	62	145	54.5	4.1	68	20.6	1.0
	FEX	83	199	54.3	5.3	82	8.5	-9.1
	AMIRZ	64	160	52.5	3.2	72	25.0	3.1
	LIFT	75	181	53.0	3.3	80	16.2	-1.3
	X	326	798	51.5	3.2	349	19.6	-.4
Israel	CHASHMAN	58	193	52.3	3.4	66	7.6	-10.2
	SHAFAN	55	136	43.4	.6	62	24.2	1.0
	PIRCHACH	69	181	47.5	.1	74	6.8	-11.2
	AMIR	76	211	48.8	1.5	73	17.8	-2.3
	GYUS	60	171	52.6	3.4	69	11.6	-7.1
	X	318	892	48.9	1.8	344	13.6	-6.0

Table 12. Sire and strain means (X) and predicted differences (PD) for production traits.

Strain	Sire	No. of Days in Persis-			Milk (kg)		Fat (kg)		Fat (%)	
		records	milk	tency	X	PD	X	PD	X	PD
U.S.	FORD	110	283	.74	9590	768	295	10	3.15	-.16
	STREAM	67	297	.73	9022	458	285	8	3.26	-.08
	ADMIRAL	122	294	.74	8946	241	291	6	3.32	-.02
	LE-DEL	54	302	.78	9510	533	289	8	3.11	-.11
	SHADE	64	286	.75	9055	337	288	6	3.26	-.06
	DAN-VER	118	292	.75	9036	351	287	7	3.26	-.05
	X	535	292	.75	9193	448	289	7	3.23	-.08
Canada	STARLITE	75	291	.76	8740	29	289	6	3.40	.07
	CAMP	69	276	.76	8746	145	285	7	3.35	.02
	SHEIK	91	266	.78	8481	-231	284	2	3.44	.12
	LESTER	112	266	.76	8714	-8	289	6	3.40	.07
	BRENT	77	300	.75	9145	396	286	6	3.19	-.08
	X	424	280	.76	8765	66	287	5	3.36	.04
N.Z.	SHAMROCK	73	243	.74	7762	-864	267	-11	3.55	.23
	BLAIR	89	275	.71	8456	-434	277	-7	3.35	.09
	ASHTON	96	272	.74	7770	-953	271	-14	3.58	.23
	MAHANA	70	270	.73	8289	-569	279	-5	3.44	.17
	MIKE	98	262	.75	7627	-868	266	-12	3.59	.21
	X	426	264	.73	7981	-738	272	-10	3.50	.19
Sweden	SLASS	64	271	.77	8537	-248	284	0	3.43	.10
	FRANKT	102	282	.75	8377	-199	278	-2	3.40	.05
	FEX	137	290	.76	8829	66	291	8	3.38	.07
	AMIRZ	105	267	.76	8581	-154	285	2	3.40	.09
	LIFT	121	291	.78	8728	-15	286	2	3.35	.03
	X	529	280	.76	8610	-110	285	2	3.39	.07
Israel	CHASHMAN	108	301	.77	9530	671	292	11	3.13	-.12
	SHAFAN	89	290	.76	9470	749	301	16	3.26	-.09
	PIRCHACH	111	296	.76	9399	745	303	20	3.30	-.08
	AMIR	114	288	.77	9433	698	300	15	3.24	-.08
	GYUS	110	305	.76	10044	1206	310	25	3.15	-.09
	X	532	296	.76	9574	814	301	17	3.22	-.09

The ranges of sire and strain means were 7 and 3%, respectively. RPT for production traits ranged from 67 to 81%. The ranking of the strains for milk and fat production from highest to lowest was IS, US, CA, SW, and NZ. The ranking for percent fat was reversed. The ranges of PD's were 2159 kg milk, 38.9 kg fat and .39% fat. The ranges of strain effects were 1551 kg milk, 27 kg fat and .28% fat.

Within-strain correlations between sire evaluations for milk in each of the countries of origin and evaluations in Israel were .84, .51, .01, .80, and .93, for US, CA, NZ, SW, and IS, respectively. Only the correlations for US and IS were significantly different from zero, but each correlation was based on only five or six pairs of observations. Expected correlations assuming no genotype x environment interaction ranged from .85 to .89. At $p < .1$ only the correlation for NZ was significantly different from its expectation, giving positive indication of a genotype x environment interaction.

The correlation between PD's for DIFF and MORT was .89 as sire of the calf and .87 as sire of the cow, in correspondence with the results of Ron, Bar-Anan, and Weller (1986) for the general Israeli population. The correlation between CULL and milk production was -.81, indicating that low production was the main cause of culling. Body size and dairy character were positively correlated with milk and fat production. Udder conformation traits were not correlated with production traits.

The sires tested were a small sample of proven sires from the donor countries. Thus differences among strains in this experiment

are not reliable estimates of the relative genetic levels of the countries represented. Nevertheless, differences among strains were large, compared with differences among sires within strains for most of the traits analysed. Significant differences among strains at $p < .01$ were found for all traits analysed. Except for IS, the cows tested were the result of between-strain crosses, and therefore the results obtained may be confounded with heterotic effects. Positive heterosis effects have been documented for production traits both for crosses between breeds and strains. It should also be noted though that some of the US and Swedish sires tested may be related to Israeli sires used in the general population (Bar-Anan, Ron, and Weller; 1987).

Milk and fat production were computed as annualized yields, corrected for days open, and extended if incomplete using factors calculated from the Israeli population by Bar-Anan, Weller, Wiggans and Osterkorn (1986); and Weller, Bar-Anan, and Osterkorn (1985). Persistency was nearly equal for all strains except NZ, which was slightly lower. Thus PD's computed for 305-day yields, uncorrected for days open, would have been nearly equal to those for annualized yields, except the 305 day PD's for NZ, which would have been slightly lower.

Mean production was more than twice the level obtained in the Polish experiment for milk and 90% higher for fat, while fat percent was 16% lower (Stolzman et al., World Anim. Rev. 38:9, 1981). The range of milk production for these strains was 18% of the mean in the

current experiment, but only 8% in Poland. Similarly for kg fat, ranges were 10 and 6% of the mean in Israel and Poland, respectively. The difference between the means of kg milk for IS and NZ were 1563 in Israel and 89 kg in Poland. The nearly complete negative correlation between PD's for milk and fat production and percent fat is also at variance with the Polish results. In the Polish experiment, NZ was third for milk production, second for fat production, and first for percent fat of the strains tested in Israel. In Israel, NZ was still first for fat percent, but last for milk and fat production. Of all the strains tested, NZ was the only one without a positive correlation of evaluations in the country of origin and PD in Israel. These factors indicate a strong genotype x environment interaction for daughters of NZ sires. Management conditions and production level in New Zealand and Poland are similar, in that both countries rely heavily on forage feeds, and different from those in Israel. This may explain why NZ sires with high PD's evaluated under extensive management did not achieve similar performance under conditions of intensive management. There is no indication from these results whether sires evaluated under intensive management will achieve similar performance under extensive management. The high positive correlations between sire evaluations for milk production in IS and US, CA, and SW may provide a basis for comparison of sire evaluations among these countries, and would be useful for comparison of genetic base differences among these countries.

B. Bidirectional selection for milk production and age of female maturity in rats.

Ron, Cahaner, and Drori (1987) bred four lines of rats from the same population for high and low milk production and early and late sexual maturity. Growth rate was higher, and sexual maturity earlier in the high, as opposed to low production line. Growth rate, body fat content and milk production of the early maturing line were higher than that of the late maturing line. F-1 and F-2 milk production of both reciprocal crosses were near the midpoint of the parent lines, while age at sexual maturity of the crosses was as late as the late maturing and low production lines. Body weight of the crosses was greater than all four parental lines. These results indicate that although most genes that advance puberty also increase milk production, not all genes that increase milk production affect age at maturity; that the genetic control of milk production is additive; that the genes that increase age and body weight at sexual maturity are dominant; and that there is heterosis for body weight at sexual maturity.

Objective 4. Genetic and environmental studies on health traits

A. Analysis of general health traits in the US.

Lyons, Freeman, and Berger (1987) studied incidences of 14 health related traits collected from 114 herds in Wisconsin, Minnesota, and Iowa by 21st Century Genetics Coop. The health data, collected under field conditions, consisted of 3664 records collected by dairymen as the cows experienced problems (producer data), and 7344 records copied (copied data) from existing data by 21st Century personnel. The producer data were more complete.

Table 13 gives the mean incidences of the individual traits recorded. The most frequent problems were mastitis, followed by uterus infections. Table 14 lists the traits grouped into body systems and the repeatability estimates for the combined data by body systems. Repeatability for the sum of all traits (unweighted) was .26.

Cows had multiple records. This presented a problem for analyses of heritabilities and genetic correlations. The covariance among records within cow was not negligible, as indicated by the repeatability estimates. The model for analysis included herd-year of freshening, sire and residual. The data were analyzed by lactations and the results pooled across lactations by the reciprocals of their sampling variances. Multiple trait REML solutions were obtained for the variance components. For some individual traits and traits grouped

Table 13. Means and standard errors of individual traits, by data set.

Trait	<u>Producer Data</u>		<u>Copied Data</u>	
	Mean	SE	Mean	SE
Sold open	.203	.007	.049	.003
Abortion	.025	.003	.018	.002
Cystic ovaries	.058	.004	.100	.004
Retained placenta	.092	.005	.024	.002
Uterus infection	.147	.006	.143	.004
No. of Inseminations	1.58	.019	1.61	.014
Other Reproductive Problems	.086	.005	.139	.005
Mastitis	.487	.016	.195	.007
Udder Injury	.113	.005	.023	.002
Other Udder Problems	.053	.004	.006	.001
Milk Fever	.094	.005	.037	.002
Ketosis	.066	.004	.020	.002
Displaced Abomasum	.022	.002	.010	.001
Other Digestive Problems	.035	.004	.013	.001
Trimmed Feet	.088	.005	.107	.004
Leg Problems	.046	.003	.032	.002
Foot Problems	.050	.004	.053	.003
Crampy	.032	.003	.005	.001
Other Locomotive Problems	.012	.002	.001	.001
Pneumonia	.014	.002	.007	.001
Other Respiratory Problems	.012	.002	.003	.001
All Other Problems	.041	.004	.012	.001
Reproductive	1.88	.020	1.91	.014
Mammary	.653	.019	.224	.008
Digestive	.217	.009	.080	.004
Locomotive	.228	.010	.199	.007
Respiratory	.026	.003	.010	.001
All summed	3.05	.035	2.43	.019
All weighted	16.13	.177	14.14	.111

Table 14. Individual traits included in each grouped trait with repeatability estimates.

Individual Trait	Grouped Trait	Repeatability
Abortion		
Cystic Ovaries		
Retained Placenta	Reproductive	.14
Uterus Infection		
No. of Inseminations		
Other Reproductive Problems		
Mastitis		
Udder Injury	Mammary	.36
Other Udder Problems		
Milk Fever		
Ketosis	Digestive	.15
Displaced Abomasum		
Other Digestive Problems		
Trimmed Feet		
Leg Problems		
Foot Problems	Locomotive	.55
Crampy		
Other Locomotive Problems		
Pneumonia		
Other Respiratory Problems	Respiratory	.19
Sum of All Traits		.26

by body systems, the smallest subclass size times the incidence rate was greater than unity. In this case the binomial is a sufficient approximation to the normal distribution, which is assumed in the REML analyses.

Table 15 lists heritability estimates for the grouped traits pooled across lactations. Estimates for reproductive and respiratory traits were very low, higher for the digestive and locomotive traits, and intermediate for mammary traits. For the sum of all traits the

estimate was .17 for the producer data, but .02 for the copied data.

Producer data were more reliable because they were more complete.

Table 15. Heritability estimates of grouped traits including only one record per progeny pooled across lactations, by data set.

Trait	Producer Data		Copied Data		Combined Data	
	h^2	Approx SE	h^2	Approx SE	h^2	Approx SE
Reproductive	.02	.04	.02	.04	.02	.03
Mammary	.12	.06	.02	.04	.07	.04
Digestive	.21	.08	.01	.04	.17	.06
Locomotive	.16	.07	.02	.04	.08	.04
Respiratory	.02	.04	.01	.03	.01	.03
All Summed	.17	.07	.02	.04	.07	.04
All Weighted	.07	.06	.01	.04	.03	.03

Table 16 gives the phenotypic and genetic correlations among grouped traits and ME milk and fat from the producer data. Generally, genetic correlations were higher than phenotypic correlations. Genetic correlations were antagonistic for reproduction and production; $-.27$ and $-.25$ for milk and fat, respectively. For all other traits with milk the estimates were positive; for all summed, $.29$; and all weighted by economic values, $.31$. For fat, the estimates were all negative except locomotive; for all summed traits, $-.25$; and all weighted, $-.06$. The reasons for these differences between milk and fat is not understood.

Table 16. Genetic and phenotypic correlations between grouped traits and ME milk and ME fat.

Trait	Correlations			
	Genetic		Phenotypic	
	Milk	Fat	Milk	Fat
Reproductive	-.27	-.25	.16	.15
Mammary	.18	-.06	-.03	-.05
Digestive	.44	-.06	.02	.02
Locomotive	.48	.45	.06	.05
Respiratory	.02	-.39	.02	-.01
All summed	.29	-.25	.10	.08
All weighted	.31	-.06	.15	.14

Table 17 lists the estimates of phenotypic and genetic correlations among grouped health traits from the producer data. The genetic correlations were all positive, except for reproductive with mammary and respiratory traits. Reproductive with locomotive was essentially zero, while all others were large and positive. Phenotypic correlations were small. Generally health problems in all body systems, except with reproductive indicate that health problems tend to be highly associated on a genetic basis. Selection for reduced health traits recorded on farms could be effective, but recording should be complete. Data should be analyzed by multiple trait BLUP.

Table 17. Genetic (above diagonal) and phenotypic (below diagonal) correlations among grouped traits using producer data.

	Reproductive	Mammary	Digestive	Locomotive	Respiratory
Reproductive	-	-.11	.38	.02	-.23
Mammary	-.03	-	.52	.84	.34
Digestive	.04	.05	-	.87	.76
Locomotive	.01	.09	.12	-	.74
Respiratory	.03	-.01	.08	.01	-

B. Analysis of reproduction related diseases in Israel.

Dr. O. Distle on Sabbatical from the Munich Veterinary Institute analyzed data on six reproductive syndromes in 102 Kibbutz herds with 76,170 recorded calvings. The syndromes studied were retained placenta, lochia (vaginal discharge during the first two weeks after parturition), endometritis, anestrus postpartum, ovarian cysts with anoestrus, ovarian cysts with nymphomania. Frequency was highest for anestrus postpartum, .35. The frequency of all other syndromes was under .10. The same analysis model was used for all syndromes, and two additional traits: all diseases, and number of disease occurrences during the lactation. The effects of HYS, sire, cow's age, days pregnant, and the interaction between the sex of the previous calf and the difficulty of the calving were included in the model. Only the sire effect was random. Coefficients of determination ranged from .05 for retained placenta to .23 for anestrus postpartum. HYS explained more of the variance than any of the other effects in the model. All

heritabilities were under .03, except third parity heritability for anestrus postpartum, which was .04. Genetic correlations among retained placenta, lochia and endometritis were $> .6$. Genetic correlations among the other syndromes were lower. Although recording in this data set was more reliable than most previous data sets used to estimate genetic parameters for disease traits, heritabilities were not significantly higher than previous estimates.

C. Analysis of somatic cell concentration and its relationship to udder infection in Israel.

Weller (1988c) analyzed environmental effects on somatic cell concentration (SCC) in Israel from 30,000 lactation records with at least one SCC estimate during the lactation. Mean SCC was about 450,000 cell/ml. SCC was lowest during the second month post partum, and increased during the remainder of the lactation. SCC increased with parity up to sixth. Correlations between the log of SCC in consecutive months were from .45 to .63. Correlations between log SCC four months apart were from .32 to .53. Correlations among actual SCC were lower.

7047 cows in 24 herds were both scored for SCC and tested bacteriologically for udder infection. Log SCC scores prior and after bacteriological assay, the mean of these scores, and the mean of all SCC scores during the lactation were analysed as functions of herd, parity, and infection status, i. e., presence or absence of bacterial

growth in the sample. Days in milk when SCC was scored was included in all analyses, except the last. All effects included in the models were significant. SCC was higher for infected cows, as expected. The coefficient of determination was highest for the mean of the two SCC scores nearest in time to the bacteriological test, 0.35. The difference between infected and non-infected cows for this analysis was 0.31 on the log scale, which corresponds to a factor of two on the linear scale. Less than 5% of cows with SCC of less than 160,000 in the milk sample taken after the bacteriological assay were infected, while 25% of cows with SCC above 400,000 were infected.

D. Analysis of the causes of cow culling in Israel.

Studies on criteria for cow culling in Israel centered on the identification of genetic relationships that exist between cow culling and its main causes; low production, infertility and mastitis. Sires were evaluated in Israel for first and second parity daughter culling. Each parity was analyzed separately. Sires were grouped by year of birth, but the analyses were conducted on sire solutions, rather than the sum of sire and group effects. This was done to obtain a meaningful comparison between younger and older sires. Since there is a positive genetic trend for production, older sires would tend to have a higher culling level than younger sires. Correlations of sire solutions for culling and sire evaluations for production,

fertility and mastitis were used to estimate genetic correlations between these traits.

First parity culling was found to be highly correlated genetically only with low production. Genetic correlations between second parity culling, first parity culling and the other traits were all low, but in the expected directions; that is, daughters of sires with higher culling rates have lower milk production and fertility and higher mastitis rate. Further study is necessary to determine useful criteria for between cow selection.

Objective 5.. Analysis of secondary traits and optimization of the
breeding program

A. Genetic analysis of calving traits in the US and Israel.

Dejemali, Berger, and Freeman (1987) developed iterative mixed-model procedures for analysis of an ordered categorical response, such as calving difficulty score, based on a threshold model in which an underlying continuous scale is assumed. Clutter and Berger (1987) studied whether ordered categorical analysis procedures (OC) are preferable to mixed linear model analysis when progeny information is limited, as in analysis of records on a bull's first-crop calves. Data from the 1986 NAAB calving ease sire evaluation included 374 sires with over 500 progeny records. Data sets were created to include exactly 500 randomly sampled records for each of the 374 sires (DATA500), and 50 records for each of the same sires (DATA50), randomly sampled from DATA500. Progeny information included in DATA500 was assumed to be sufficient for accurate prediction of true transmitting ability. The mixed model for OC included random effects of sires and herd-years, and the fixed effects of sex of calf, parity of dam, and season across herd-years. Herd-year-seasons (HYS) were fixed in the BLUP analysis. Sires were grouped by birth year and each analysis included the inverse of relationships. Product-moment correlations between OC sire solutions for DATA50 and DATA500, BLUP sire solutions for DATA50 and OC sire solutions for DATA500, and BLUP

and OC sire solutions for DATA50 were .72, .67, and .94, respectively. Corresponding rank correlations were .70, .66, and .92, respectively. The OC is conceptually the more appropriate analysis, and yields direct probability statements concerning sire's calving ease, which is not given directly by BLUP evaluations.

The analyses were also applied to an extensive set of data supplied by the National Association of Animal Breeders; over 1.3 million calving records and 11,442 sires. Advantages of a threshold model (TM) were demonstrated. The distribution of sire solutions by the TM analysis was more symmetric with a greater range of values than those of a linear model (LM) analysis. Genetic trends were evident in the linear model analysis, but there was no evidence of any genetic trend in the sire solutions from the TM analysis. Non-normality of the data resulted in greater differences among the average of sire solutions over time, but when the data were corrected for non-normality by the TM analysis, there was no evidence of any genetic trend.

Sires ranked about the same by both analysis procedures. The correlation among sire solutions was .90. Larger changes in rank were observed among those sires with few progeny by heifers. BLUP and TM sire solutions were transformed to a probability scale so that the calving ease proof for each bull could be reported as the expected percent of difficult births in matings to heifers. BLUP solutions were transformed by a linear prediction equation determined by the regression of BLUP solutions on the actual percentage of difficult

births in heifers. Four probability statements, however, are possible with the TM analysis depending on the sex-of-calf and season-of-birth. The predicted probability of a male calf born with difficulty in the winter season was found to be better than probability statements averaged over sex-of-calf, season-of-birth or all four combinations for sex-of-calf and season-of-birth. We tended to favor the "worst-case" scenario because the mean percentage was higher and there was a greater range in values for the expected percentage. Therefore, dairy farmers might have more of an opportunity to pick and choose among individual bulls. Sire solutions were highly correlated with the expected percent of difficult first calvings. The correlation was .95 for the BLUP analysis, and .97 for the TM analysis. The correlation between BLUP sire solutions and expected percent of difficult first calvings by the TM analysis was .90. All Holstein sires in the US are now evaluated at Iowa State University using the mixed-model for ordered categorical responses with a threshold model.

Ron, Bar-Anan, and Weller (1986); Weller, Ezra, and Bar-Anan (1986); Weller, Misztal, and Gianola (1988) and Weller and Gianola (1989) studied calving traits in the Israeli Holstein population. Calvings of 106,751 Israeli heifers were analyzed for dystocia and calf mortality, scored dichotomously, and a composite trait scored trichotomously. Dystocia was also studied with 146,973 second and third parity records. Data was analyzed by both linear and threshold models. Models fitted included HYS, sex of calf, calving age, calving month, sire of cow, sire of calf, and groups of sire of cow and of

calf. HYS, sire of cow and calf, and residuals were random, with diagonal variance-covariance matrices. HYS variance was assumed to be 10% of the residual component. Other variance components were estimated by REML for the LM analyses and by the counterpart of REML for the TM analyses. Heritability estimates were two to five times greater in threshold than in linear models, but correlations between corresponding sire evaluations were all $>.9$. LM sire evaluations were skewed positively, whereas TM evaluations had symmetrical distributions. Heritability for dystocia was greater in first than in later parities. Correlations between first and later parity sire evaluations were $<.5$. Thus, the genetic control of dystocia seems to be different for heifers and cows. Correlations between sire of cow and calf evaluations were $<.3$. Correlations between dystocia and calf mortality evaluations were $\sim .7$.

B. Effects of body measurements and weight on calf size and calving difficulty.

Sieber, Freeman, and Kelley (1989a) used data from the Ankeny research herd to associate body measurements, body weight, and calving problems. Body measurements (heart and paunch girths, wither height, chest depth, pelvic length and width, and body length), body weight, and calving evaluation data (calf birth weight, calf sex, calf presentation, and calving assistance needed) were collected from 1794 parities of 762 Holstein cows between 1968 and 1986. Degree of

calving assistance was scored continuously from 1 (no assistance) to 10 (hard mechanical assistance). Phenotypic correlations of dam body traits with calf birth weight were all significantly positive when combined for all parities, and ranged from .23 for paunch girth to .27 for body weight and heart girth. Correlations of dam body measurements and weight with calving assistance scores were all significantly negative across parities, and ranged from -.24 to -.30. Correlations of calf birth weight with calving assistance were higher for first parity (.37) than for all parities (.20). Least squares analysis showed that cows with shorter wither height and shorter pelvises tended to require more calving assistance. Heavier calves, winter calvings, earlier parity, and posterior calf presentation all were related to increased dystocia. Male calves were heavier than female calves, and also were associated with greater calving difficulty.

C. Genetic and environmental relationships between fertility and production in Israel and the US.

Despite the economic importance of fertility in dairy cattle there has been little emphasis on breeding for either male or female fertility, since heritability for most measures of fertility is low. Because the field data generally available consist of insemination dates, most studies have estimated female fertility by non-return rates, the number of times a cow is bred during a lactation, or by

days open. Several studies found negative genetic correlations on the economic scale between fertility and production traits, while others found no significant relationships. Fertility traits are problematic for genetic analysis. Cows that do not conceive do not have a value for days open. Therefore studies that have analyzed days open have either deleted cows that did not conceive from the analysis, or used a "pseudo" days open value, such as last insemination date or some arbitrary high value. All of these options will tend to be biased. The first approach is undesirable because cows with the most obvious fertility problems are eliminated from the analysis. Among cows that do not conceive readily, farmers will be more likely to re-inseminate those with superior milk production, or cows that are daughters of elite sires. Thus, cows with long open periods will not be a random sample with respect to either production or pedigree. Furthermore, since data on conception are not generally available, neither number of breedings nor non-return rate distinguish whether or not the cow conceived on a given insemination. Thus for cows that did not conceive, a low number of inseminations is not indicative of high fertility.

Field data collected in Israel are unique in that pregnancy is determined by veterinary examination for all cows that do not display estrus within 60 days of insemination. Weller (1989) estimated genetic and phenotypic parameters of fertility using these data, and genetic and environmental trends for fertility and production traits in the Israeli Holstein population.

Data were first through third parity insemination and production records of Israeli Holsteins inseminated between January 1, 1980, and July 31, 1986. Records were eliminated if: 1) no insemination was recorded prior to 153 days in milk; 2) days in milk were less than 34, or number of monthly tests was less than two; 3) previous parity records of the cow were missing; 4) fewer than 20 daughters per sire; or 5) otherwise abnormal. The edited data set consisted of 91,770 cows, daughters of 296 sires. This sample included daughters of the 26 sires in the international sire comparison described above. Since cows without first parity records were deleted, the number of first parity records was also 91,770.

Fertility traits analyzed were conception status (CS) [1/number of inseminations to conception], and days from calving to first breeding (DFB). Cows that were inseminated but did not conceive, as determined by veterinary examination, were scored as zero for CS. Cows with more than five inseminations were given the same score as those with five inseminations. Fertility traits were adjusted for the effect of parity, using additive adjustment factors. The frequency tables of the fertility traits for first parity are given in Table 18.

For sire evaluations, it was assumed that the sire, cow, and residual variance components were 1, 9, and 90% of the total variance for CS and DFB; and 5, 45, and 50% of the variance for milk and fat production. Groups were determined biennially by year of birth for the general population, and by country of origin for the 26 test sires. HYS effects were absorbed, while sire and group solutions were

solved by iteration. Sires were assumed to be unrelated. Sire evaluations were computed as the sum of each sire's group and sire solutions.

Table 18. Frequency table for fertility traits of 91,770 first parity cows.

No. of inseminations to conception	Conception status (%)	Frequency		Days to first insemination	Frequency	
		no.	%		no.	%
1	100	43993	48	<50	1617	2
2	50	19603	21	51-70	25594	28
3	33	9999	11	71-90	34570	38
4	25	5205	6	91-110	19238	21
>4	20	6115	7	111-130	7155	8
non-conception	0	6855	7	>130	3596	4

Variance components were estimated separately for first and second parity by Henderson's method 3 (HM3). The analysis model was the same as described above, except that a cow effect was not included, since each parity was analyzed separately. In the first parity analyses, only cows with records on all four traits were included.

First parity variance components for the four traits analyzed, as estimated by the HM3 analyses, are listed in Table 19; and the corresponding heritabilities and the genetic and environmental correlations are listed in Table 20. Heritabilities are on the diagonal, genetic correlations are above the diagonal, and environmental correlations are below the diagonal. All the genetic and environmental correlations listed are within the range of .3 to

-.3, except for the correlations between milk and fat production, which are similar to previous results of Weller, Ron, and Bar-Anan (1986) for these traits. The next highest correlation is the genetic correlation between milk production and DFB. All the remaining correlations are within the range of .2 to -.2. The genetic correlation between DFB and the production traits is similar to most previous reports on other populations. The virtually nil genetic correlation between CS and production traits is probably not significantly different from the value of -.2 found by Hermas et al. (J. Dairy Sci. 70:1252) on a small sample of Guernsey cows. However, the exact definition for this trait was different. Environmental correlations between fertility and production traits were also close to zero, similar to the results for annualized yields, and 305 day yields corrected for days open; but contrary to most previous studies that did not correct production traits for the effect of days open. Heritabilities for fertility traits are similar to most previous studies on different populations. Heritabilities for yield traits are lower than most results for Holsteins, but consistent with results of Weller, Ron and Bar-Anan (1986).

First and second parity heritabilities for the fertility traits, and the genetic and environmental correlations between first and second parities for these traits, are listed in Table 21. Heritabilities were slightly lower in second parity. Similar to previously published results, genetic correlations were $> .7$ while environmental correlations were $< .1$. Although genetic control of

different parities is not identical, it is similar, and the assumption of a common sire component of variance for all parities employed in the analysis model seems reasonable. Conversely, since both heritability and the environmental correlation are low, and selection is based on actual performance, second parity results should not have been appreciably biased by selection.

Table 19. First parity (co)variance components for conception status (CS), days to first breeding (DFB) and production traits.

Variance component	Trait	Conception status (%)	Days to first insemination (days)	Milk ₂ (kgx10 ²)	Fat (kg)
Sire	CS	10.66	-.18	-.14	-.81
	DFB		4.38	1.32	2.29
	milk			5.32	10.57
	fat				32.03
Residual	CS	1220.8	18.0	10.4	57.2
	DFB		362.9		9.4
	milk			152.5	354.8
	fat				1116.0

Table 20. Heritabilities (on the diagonal), genetic correlations (above the diagonal), and environmental correlations (below the diagonal) among first parity fertility and production traits.

	CS	DFB	Milk	Fat
Conception status	.035	-.026	-.019	-.044
Days to 1st breeding	.027	.048	.271	.194
kg milk	.024	.045	.135	.81
kg fat	.049	.015	.86	.112

Table 21. Heritabilities and genetic and environmental correlations for first and second parity fertility traits.

	Conception status	Days to 1st breeding
Heritability, parity 1	.035	.048
Heritability, parity 2	.022	.031
Genetic correlation	.792	.732
Environmental correlation	.090	.061

The frequency tables of the sire evaluations for CS and DFB are given in Table 22. The 26 sires evaluated in the international sire comparison were deleted from this table. The range of RPT was from .22 to .98, with a mean of .56. Even though the heritability of CS was < .04, more than 10% of the sires were outside the range of -4 to 4% for CS. Of these sires, 16 (53%) had RPT > .5. Thus real genetic differences do exist for these traits, as previous studies have indicated.

Table 22. Frequency table of 273 sire evaluations for fertility traits.

<u>Conception status (%)</u>			<u>Days to first insemination</u>		
<u>range</u>	<u>frequency</u>		<u>range</u>	<u>frequency</u>	
	no.	%		no.	%
<-4	14	5	<-2	17	6
(-4)-(-2)	38	14	(-2)-(-1)	57	21
(-2)-0	91	33	(-1)-0	71	26
0-2	76	28	0-1	58	21
2-4	38	14	1-2	54	20
>4	16	6	>2	16	6

Holstein strain differences for the Israeli, US and Swedish sires from the international sire comparison are given in Table 23. Canadian and New Zealand sires were not significantly different from the Israeli sires for CS, and are therefore not presented. Swedish sires were most favorable for fertility, but low for production traits. Israeli sires were highest for production, but intermediate for fertility; while US sires were lowest for fertility, and intermediate for production. Although the differences between the strains were significant ($p < .01$), the strain effects are based only on 5-6 sire elite sires from each country. These differences may reflect different national selection criteria. In Israel breeding has been for annualized yield adjusted for days open (Bar-Anan, J. Sci. Agri. Soc. Finland, 55:489, 1984), while in the US breeding has generally been for 305-day yield, unadjusted for days open (Dickenson et al., Agric. Res. Serv., USDA Prod. Res. Rep. No. 165:18). Since the genetic correlation between 305-day yields and days open is positive, selection in the US for high yields may have led to selection for low conception rate.

Table 23. Holstein strain differences for production and fertility.

Traits	Strains		
	Israel	U. S. A.	Sweden
Conception status (%)	3.32	-2.24	9.44
Days to 1st insemination	1.24	-.60	-1.25
kg milk	817.9	432.1	-103.4
kg fat	16.5	6.8	2.4

Valente and Berger (1988) and Van Raden, Freeman, and Berger (1987) studied the genetic and environmental relationships between fertility and production traits in US Holsteins. Variance and covariance components were estimation by multi-trait REML in an unequal information setting. The objectives were: 1) to compare estimation procedures; and 2) to study the genetic and environmental relationship among 305d ME milk yield, number of services per conception in cows, and number of services per conception in heifers. Estimates were obtained by two forms of an expectation maximization algorithm (EM1 and EM2) and a third shortcut algorithm (SHC) which uses expectation maximization for the within sire component and the "method of scoring" for the between sire component.

Data were 49,918 cows with mature equivalent 305d milk yield and number of services, of which 15,656 cows also had number of services as heifers. Two separate analyses were conducted to study the effect of the unequal number of traits per cow. The missing data case included all cows, with or without number of services as heifers, and the equal data case included only cows with number of services as a heifer and cow. The model included fixed HYS, random sires and residual. There were 352 sires in the missing data case and 327 sires in the equal data case. Sires were assumed to be unrelated.

Many changes in estimates of variance and covariance components were evident by including all data. The variance among sires increased for milk yield, while all other genetic variances and covariances decreased. There were larger changes in variances and

covariances among sires than within sires. The largest percentage change was observed for the covariance between milk yield and number of services as heifers.

The net effect of changes in estimates of heritabilities is in Tables 24. A definite advantage to using all data, and an analysis procedure which accounts for missing traits was clearly demonstrated. Heritability increased for milk yield, and decreased for number of services in cows and heifers.

Table 24. REML heritability estimates, with observations with missing records included (I) and deleted (D).

Trait	<u>Missing records</u>		difference (I - D)	<u>I - D</u> D
	I	D		
ME 305d milk yield	.221	.141	.08	.57
Number of services, cows	.016	.023	-.007	-.03
Number of services, heifers	.013	.014	-.001	-.07

The net effect of changes in estimates of genetic correlations is in Table 25. All genetic correlations decreased with the largest decline in the genetic correlation between milk yield and number of services in heifers. A positive genetic correlation between milk yield and number of services in cows is interpreted as an antagonistic correlation. The antagonism is due in part to the stress of high milk yield causing cows to be less fertile. This analysis reconfirms the earlier work of Hansen and others (BARD project I- 3-79). We have placed the estimate more in line with the underlying biological relations among the traits studied.

Table 25. REML estimates of genetic correlations among mature equivalent 305 day milk yield (ME 305), and number of services for cows (NSC) and heifers (NSH), with observations with missing records included (I) and deleted (D).

Traits	<u>Missing records</u>		difference (I - D)	<u>I - D</u> D
	I	D		
ME 305, NSC	.302	.591	-.289	.49
ME 305, NSH	-.244	.073	-.317	-4.34
NSC, NSH	.429	.683	-.254	-.37

The discrepancy between the results of the US scientists, who found an economically negative genetic correlation between cow fertility and production; and the Israeli scientists, who did not, was not resolved. It should be noted, though, that the populations analyzed, the definitions of the traits analyzed, and the statistical methods used in the two countries were all different.

D. Genetic, environmental and phenotypic trends for production and secondary traits.

Weller, Ron, and Bar-Anan (1986); and Weller (1989) estimated phenotypic, genetic, and environmental trends for production and fertility traits in the Israeli Holstein population. Phenotypic trends for production and fertility traits in Israel were computed as the regression of each cow's first parity record on her first parity calving date. Genetic trends were estimated as twice the regression of each cow's sire evaluation on the cow's first parity calving date. Environmental trends were estimated as the difference between the

phenotypic and genetic trends. Trends for milk and fat production were estimated over two time periods; 1976 through 1985, and 1980 through 1986. The procedure of doubling sire evaluations, which assumes equal genetic progress on the dam side, although commonly used for production traits may in fact be an overestimate, since progress in the dam line tends to lag behind progress in the sire line.

The genetic, environmental and phenotypic trends are listed in Table 26. Genetic trends for milk and fat production were greater during the later time period; while environmental trends were positive during the earlier time period, and negative during the later period. Genetic trends were economically positive for milk, fat, and economically fat corrected milk (FCM) production, and for conception status; and negative for fat percent and days to first breeding. If the genetic correlation between production and conception status was negative, and the genetic trend for production was positive, then the genetic trend for conception status should have been negative. Although the numbers of cows and sires were relatively large, the number of progeny per sire vary greatly, and a few sires with many daughters could have had major effects on the values presented. The reason for negative environmental trends during the later period may be due to stricter implementation of production quotas during the later years.

Table 26. Genetic, environmental and phenotypic trends in the Israeli dairy population from 1980 through 1986.

Years studied	Traits	Trends		
		genetic	environmental	phenotypic
1976-85	Milk (kg/yr)	89.	84.	173.
	Fat (kg/yr)	2.16	4.48	6.64
	Fat (%/yr)	-.008	.23	.015
	FCM (kg/yr)	81.	102.	183.
1980-86	Milk (kg/yr)	154.	-38.	116.
	Fat (kg/yr)	3.03	-.45	2.58
	Conception status (%/yr)	0.96	-1.01	-0.05
	Days to 1st breeding (dy/yr)	0.09	-0.72	-0.63

E. Genetic and environmental parameters of milk composition in Israel.

The laboratory of the Israeli Dairy Union began extensive testing of milk protein concentration of individual cows in 1985. This data is automatically recorded on computer diskettes and has been made available for analysis. Drori and Ron (1988); Ezra, Raz, and Weller (1988); Ezra, Weller, and Drori (1987); and Ron, Ezra, and Drori (1988) studied environmental and genetic factors affecting protein production and concentration. 33,185 first through third parity lactation records from 105 herds that passed edits were analyzed. Means of fat and protein monthly tests were 3.2% and 3.0%, respectively. Standard deviations were .6% and .3%. Fat and protein concentration was lowest during the peak production post partum period, and increased with the cows' parity, in correspondence with

results from other countries. Peak production and fat percent were concurrent in the winter, while peak protein production was in the late autumn. These results are in correspondence with results found in the US (Hillers, 1974, J. Dairy Sci. 57:444).

Mean annualized protein production was 282 kg for Kibbutz (communal) herds, and 257 kg for Moshav (family) herds. The standard deviations were 41 and 35 kg, respectively. Means for protein concentration were $3.03 \pm .12$ and $3.17 \pm .20$ for Kibbutz and Moshav herds, respectively. Ratios of protein to fat production were .965 and .977, respectively. After correction for milk production level, fat percent was equal at both farm types, while protein production was still higher at Moshav farms. Significant differences among farms were found for both fat and protein production.

Variance components and genetic evaluations were computed by Henderson's method 3 on a subset of 9815 cows, daughters of 85 sires from 382 herd-years. Estimates of heritabilities, genetic and environmental correlations among milk, fat, protein, and fat and protein concentration are presented in Table 27. These estimates are similar to results of several studies for the US Holstein population. Heritabilities for milk and fat production were slightly higher than the estimates of Weller, Ron, and Bar-Anan (1986) for the Israeli population. The genetic correlations between fat percent, and milk and fat production were higher than the previous study, which was conducted on a more extensive sample. These estimates were used to predict future genetic trends for the Israeli population.

Table 27. Heritabilities (on the diagonal), genetic correlations (above the diagonal), and environmental correlations for production traits in the Israeli population.

	Milk (kg)	Fat (kg)	Protein (kg)	Fat (%)	Protein (%)
Milk (kg)	.17	.63	.76	-.13	.44
Fat (kg)	.69	.25	.67	.68	.05
Protein (kg)	.92	.76	.16	.0	.25
Fat (%)	-.28	.47	-.05	.29	.40
Protein (%)	-.35	.05	.05	.51	.46

Under Israeli conditions of surplus fat production and importation of powdered skim milk, protein production is more important economically than butterfat. It is therefore recommended that protein be included as a major breeding objective once reliable sire evaluations become available.

F. Relationships between body measurements, body weight, and productivity in Holsteins.

Sieber, Freeman, and Kelley (1989a) analyzed data from the Ankeny research herd, which is used to select for high and average milk production, in order to estimate relationships between body measurements, body weight and estimated feed efficiency. Means of actual (not mature-equivalent) production variables and estimated feed efficiency, are given in Table 28, and coefficients of variation in Table 29. Estimated feed efficiency (EFE) was computed as milk energy content divided by net energy consumed, and expressed as megacalories

of milk energy content divided by megacalories of net energy. Efficiency was not measured directly, but was estimated on a lactation basis. Actual yields were converted to a 4% FCM basis to express energy in milk, and feed requirements were calculated from the 1978 NRC requirements. All weights and measurements increased through the fifth parity, and actual milk production peaked in fourth parity.

Table 28. Means of milk, fat, fat corrected milk production (FCM), fat and solid-not-fat (SNF) concentration, and estimated feed efficiency (EFE) by parity.

Parity	N	Means					
		Milk (Kgs)	Fat (kgs)	FCM (Kgs)	Fat (%)	SNF (%)	EFE (%)
1	765	5531	202	5242	3.66	9.25	.587
2	484	6871	252	6527	3.71	9.12	.570
3	313	7137	263	6800	3.71	9.08	.578
4	177	7247	265	6880	3.68	9.01	.577
>5	159	7153	263	6809	3.68	9.04	.573
All	1898	6433	236	6111	3.68	9.15	.579

Table 29. Coefficients of variation of milk, fat, fat corrected milk production (FCM), fat and solid-not-fat (SNF) concentration, and estimated feed efficiency (EFE) by parity.

Parity	N	Coefficients of variation (%)					
		Milk (Kgs)	Fat (kgs)	FCM (Kgs)	Fat (%)	SNF (%)	EFE (%)
1	765	32.52	32.24	31.92	11.48	3.90	10.34
2	484	27.02	25.42	25.55	11.08	4.12	10.10
3	313	26.23	25.76	25.40	10.95	4.45	12.00
4	177	28.07	27.81	27.41	10.73	4.28	12.20
>5	159	28.31	28.00	27.68	10.41	3.45	10.62
All	1898	31.27	30.75	30.50	11.14	4.16	10.83

Phenotypic correlations between body measurements, body weight, production and EFE are given in Table 30. Correlations $\geq .08$ were significant at $p < .05$. Correlations among body measurements, body weight and yield were positive and significant and ranged from .18 to .29. Fat percentage was generally not significantly related to measurement and weight, while SNF percent was significantly negatively related to these traits. EFE was negatively correlated with all measurements. These correlations ranged from -.18 for wither height to -.33 for body weight. Thus taller, longer, deeper and especially heavier cows tended to not be as efficient as smaller cows.

Table 30. Phenotypic correlation coefficients among body measurements, actual production variables, and estimated feed efficiency (EFE).

Yield traits	Heart girth	Paunch girth	Wither height	Chest depth	Pelvic length	Pelvic width	Body length	Body weight
Milk (kg)	.18	.26	.22	.22	.19	.27	.21	.20
Fat (kg)	.21	.29	.24	.25	.22	.29	.23	.24
FCM (kg)	.20	.28	.23	.24	.21	.28	.22	.22
Fat (%)	.06	.09	.04	.04	.08	.06	.04	.09
SNF (%)	-.14	-.14	-.14	-.12	-.14	-.20	-.14	-.20
EFE	-.31	-.23	-.18	-.23	-.22	-.23	-.20	-.33

Phenotypic correlation coefficients between actual production variables and EFE are in Table 31. All correlations were significant at $p < .05$. Correlations $> .08$ were significant at $p < .001$. Yield and percentage traits are correlated as expected. The phenotypic correlation among EFE and yield are about .6, .05 for fat % and EFE,

and .07 for SNF percent with EFE. These data clearly indicate increased yields are associated with better feed utilization.

Table 31. Phenotypic correlation coefficients between actual production variables and estimated feed efficiency (EFE).

	Fat (kg)	FCM (kg)	Fat (%)	SNF (%)	EFE (%)
Milk (kg)	.94	.98	-.13	-.17	.61
Fat (kg)		.99	.18	-.08	.62
FCM (kg)			.05	-.11	.63
Fat (%)				.30	.05
SNF (%)					.07

Multiple regression analyses showed that cows with smaller heart girths and larger paunch girth had significantly higher yields. Taller cows produced more milk than shorter cows. Cows lighter in body weight yielded greater FCM as first-calf heifers and through all lactations. Over all parities, FCM decreased 7.8 kg for each kg increase in body weight for cows with equal body measurements.

Ron, Ezra and Weller (1987) analyzed slaughter records of 4545 male calves, sons of 38 sires, slaughtered in one central slaughter house in Israel. Heritabilities for annual growth rate and meat production were .15 and .2, respectively. Sires were evaluated for these traits, with herd and slaughter age included in the analysis models as fixed effects. The range of sire evaluations were 25 and 14 kg for annual growth rate and meat production, respectively. The correlation between sire evaluations for these traits was .9. Correlations between sire evaluations for these traits and milk

production and calving difficulty were all positive, but below .3. At the current ratio between milk and beef prices in Israel, significant selection for beef traits in the dairy population cannot be justified.

G. Genetic analysis of linear type traits and the relationship between production and type in the US.

Factor analysis is a procedure for removing redundancy from correlated variables and representing the variables with a smaller set of "derived" variables, called "factors". The objective was to investigate the potential of a common factor analysis conducted from a genetic correlation matrix instead of a phenotypic correlation matrix of linear type traits as input variables. This is the first time a genetic correlation matrix has been used in a factor analysis. A multiple-regression analysis is then used to determine how production and herd life are related to the factors computed from the phenotypic and genetic correlation matrices.

Sieber, Freeman, and Hinz (1987, 1988) applied factor analysis to data on linear type scores for 18 traits from evaluations collected by 21st Century Genetics. The first factor analysis was based on the phenotypic correlation matrix among the 18 traits. Type and production records from September 1979 to December 1983 were matched. There were 43,428 records from daughters of 228 sires with at least 20 progeny in at least 9 herds. The production variables were herd-mate deviation

milk and fat. Data for herd life were 17,288 records where herd life was days from freshening to removal from the herd. A sire model was used with fixed herd-year-seasons. Data were randomly split by herds to analyze and validate the investigation of factor analysis to relate type scores to production variables.

Type traits, scored from 1 to 50, were adjusted for days in milk and age at first calving. Means $\pm$ SD of the adjusted type scores ranged from 25.2 ± 5.39 to 31.7 ± 9.09 . A principal component analysis showed that the first eight components accounted for 69% of the total variance in the type scored. These 8 principal components had eigenvalues greater than 1.0. The remaining information in components 9 through 18 could account for some of the variation, but at some point, these components represent only random variation. The validation analysis produced very similar results to the original analysis. A principal factor analysis followed by a factor rotation was used to define new factors. Multiple linear regression on these factors indicated that herdmate deviation milk and fat are phenotypically more closely related to characteristics of the mammary system than they are to traits describing the body of the cow. The next most important traits were related to dairyness. The analysis of herd life indicated that cows with strongly supported and well attached udders remained in herds longer. Two other important traits for long herd life were dairyness plus disposition of the cow and good milkout characteristics.

Principal components (PC) were computed from both the phenotypic and genetic correlation matrices. Genetic correlations were estimated using a REML algorithm. The first PC from the genetic correlation matrix accounted for 5.6% more variation in the type traits (20.8% vs. 15.2%) than the first PC from the phenotypic correlation matrix. Using the criteria of the eigenvalue equal to one, seven genetic PC were used in the regression analysis vs. eight in the phenotypic analysis. The seven genetic PC explained 79.3% of the total variance in type traits, vs. 69.1% expressed by eight phenotypic PC.

Table 32 shows the differences between the two methods, and also where the reduction from eight phenotypic to seven genetic factors occurred. Factor pattern coefficients are listed after each factor in parenthesis. Genetic factors are ordered from largest to smallest according to the amount of variation explained in the type traits. The phenotypic factors are matched with the genetic factor that was most similar. Phenotypic factor 6 has no single genetic counterpart, and is shared among genetic factors 2, 3, and 7. The phenotypic factors did not rank the same as the genetic factors. Also, the individual traits of udder depth and fore udder attachment as phenotypic factors were apportioned to other udder traits in the genetic analyses.

Table 32. Type traits and factor pattern coefficients of the most important traits in phenotypic and genetic factors.

Phenotypic factors	Factor order		Genetic factors
	Phenotypic	Genetic	
Basic Form (.88)	1	1	Basic form (.92)
Strength of body (.84)			Strength of body (.88)
Rump width (.59)			Rump width (.51)
Body depth (.32)			Rump side view (-.56)
Stature (.36)			Dairyness (-.40)
Suspensory ligament (.84)	3	2	Suspensory ligament (.91)
Teat placement (.84)			Teat placement (.91)
			Udder depth (.55)
			Fore udder attach. (.40)
Rear udder width (.89)	2	3	Rear udder width (.91)
Rear udder height (.88)			Rear udder height (.89)
			Fore udder attach. (.67)
			Udder depth (.43)
Legs, rear view (.73)	7	4	Foot angle (.87)
Foot angle (.52)			Legs, rear view (.60)
Dairyness (.80)	4	5	Disposition (.86)
Body depth (.69)			Dairyness (.80)
Stature (.43)			
Disposition (.84)	5	6	Disposition (.85)
Milkout (.81)			Milkout (.77)
Rump side view (.83)	8	7	Stature (.91)
Stature (.42)			Udder depth (.42)
Udder depth (.70)	6	2+3+7	
Fore udder attachment (.70)			

Table 33 lists the multiple regression coefficients for the phenotypic (F1 to F8) and genetic (G1 to G7) factors, standard errors and t-values for the regressions on milk. The multiple regression analysis for fat was computed, but is not shown. Rank order of

importance of the different factors is given after the t-values in parenthesis. Significant levels are denoted as follows: * , $P<.01$; ** , $P<.001$; ns, not significant. Rank order of genetic factors, based on relative importance associated with milk and fat, shows G5 (outstanding dairyness with deep bodies) was the most strongly associated with both production traits. In both phenotypic and genetic analyses, the factors derived from dairyness and udder strength had strong associations with milk and fat. Strength of body and disposition were also strongly associated with both milk and fat on a genetic basis, but slightly less on a phenotypic basis.

Table 33. Multiple regression analysis for herdmate deviation milk by using phenotypic factors (F1 to F8) and genetic factors (G1 to G7).

Phenotypic factors				Genetic factors			
Factor	Coefficient	SE	t-value	Factor	Coefficient	SE	t-value
F1	-126.73	6.07	-20.89**(4)	G1	-130.43	5.87	-22.23**(2)
F3	37.81	8.19	5.61**(7)	G2	-110.33	6.66	-16.58**(3)
F2	201.74	7.77	25.96**(3)	G3	75.63	6.76	11.19**(5)
F7	24.54	9.53	2.58* (8)	G4	37.14	8.87	4.19**(6)
F4	373.56	9.28	40.24**(2)	G5	378.90	8.19	46.24**(1)
F5	98.82	8.54	11.58**(5)	G6	128.49	9.15	14.05**(4)
F8	73.81	12.44	5.93**(6)	G7	- 15.00	2.18	- 1.23ns(7)
F6	-488.46	11.01	-44.38**(1)				

Table 34 lists the regression results for the herdlife data. The same factor (strong well-supported udders) had the largest influence in both the phenotypic and genetic analyses based on the t-values of the regression coefficients. Next in importance in the genetic analysis were cows with extreme dairyness and deep bodies.

Table 34. Linear regression analysis for herd life by using phenotypic factors (F1 to F8) and genetic factors (G1 to G7).

Phenotypic factors				Genetic factors			
Factor	Coefficient	SE	t-value	Factor	Coefficient	SE	t-value
F1	- 1.19	1.70	- .70ns(7)	G1	- 3.81	1.63	- 2.35* (4)
F3	19.25	2.33	8.26** (1)	G2	20.21	.83	11.04** (1)
F2	2.92	2.20	1.33ns(6)	G3	3.84	.88	2.04* (5)
F7	1.54	2.62	.59ns(8)	G4	2.42	.39	1.01ns(7)
F4	9.86	2.64	3.73** (4)	G5	15.06	.31	6.53** (2)
F5	9.35	2.54	3.68** (5)	G6	3.65	.67	1.37ns(6)
F8	26.26	3.53	7.43** (2)	G7	-13.82	.37	-4.10** (3)
F6	12.77	3.11	4.10** (3)				

The main difference in these analyses on a phenotypic and genetic basis is fewer factors (7 vs. 8) were needed on a genetic basis and the latter explained more variation. Using the factor analysis 79.3% of the variation in 18 traits can be explained by 7 factors that are meaningful. Thus, scoring of cows and explanation can be simplified.

H. Genetic analysis of twinning rate in Israel.

Twinning rate was analyzed in 221,348 second and third parity calvings of Israeli Holsteins, daughters of 473 sires. Mean rate of twinning was 2.4% and heritability was 2.4%. The range of BLUP sire evaluations was 8.7%. Evaluations were positively skewed, while log-transformed evaluations were symmetrically distributed. Correlations between sire and maternal grandsire evaluations were near the expected value of .5. Thus there is no evidence for segregating major genes or nonadditive inheritance for this trait. Correlations

between sire evaluations for twinning rate and milk production, fat percent, dystocia, and carcass gain were .14, -.13, -.28, and -.34; respectively. Thus there are no indications of economically important adverse genetic correlations with twinning rate. Breeding for increased twinning rate may be feasible, by selection of high-repeatability sires with positive evaluations for twinning rate.

I. Optimization of the Israeli breeding program.

The effect of varying the number of sires progeny tested, number of cows mated to young sires, and mean number of years of service of proven sires on genetic progress for milk production was estimated with and without multiple ovulation and embryo transplant (MOET) for bull dams. The following assumptions, which approximate the conditions of the Israeli breeding program, were employed: 65,000 cows are milk-recorded out of a population of 100,000; six elite sires are used as bull sires each year; all cows not mated to young sires are mated to 20 proven sires; the phenotypic standard deviation and heritability of milk production are 1400 kg and .2; 17.5% of cows are culled due to low production; the number of bull dams is equal to two and six times the number of young sires with and without MOET, respectively; and sires used in the general population are selected after results of their daughters' first lactation, while sires of sires are selected after their daughters' second lactation.

Genetic progress was greatest when proven sires were used four years. Without MOET, maximum genetic progress, 132.9 kg/yr, was obtained when 45% of all cows were mated to 190 young sires each year. Expected genetic progress was 2% less if 25% of the cows were mated to 100 young sires, the current situation. MOET for bull dams increased genetic progress consistently by 6 to 7 kg/yr. Under the following assumptions: the value of an additional kg of milk is \$.2, a discount rate of 5%, the cost of an additional sire stall is \$3557, the cost of sire maintenance is \$876/yr, the cost of establishment of a MOET unit is \$300,000, and the cost of each ET is \$500; time to achieve the economic break even point for increasing the number of sires tested from 40 to 60 was 23 yr, and for the MOET scheme was 15 yr.

J. Expected correlated responses to changes in selection goals in Israel and the US.

The expected correlated responses to two generations of index selection for milk, fat, and conception status were estimated by Weller (1989) as follows:

$$CR_t = 2I(h)r_t(\sigma_t)$$

where CR_t is the correlated response for the t^{th} trait, I is the selection intensity, h is the accuracy of the index, r_t is the genetic correlation between the selection index and the t^{th} trait, and σ_t is the square root of the genetic variance for the t^{th} trait. I was

assumed to be equal to 1.5, which is comparable to selection of the best 17%. h and r_t were estimated as follows:

$$h = \frac{[a'GRa]^{.5}}{[a'Ga]^{.5}}$$

$$r_t = \frac{a'Gb}{\{[a'Ga][b'Gb]\}^{0.5}}$$

where a is the vector of economic weights; G is the genetic variance-covariance matrix, as estimated from the HM3 analysis; R is a matrix of order equal to G with mean sire repeatabilities on the diagonal and zero elsewhere; and b is a vector of order equal to a with an element of one for trait t and all other elements equal to zero. Mean repeatabilities were computed as follow:

$$MRPT_t = \frac{100}{(K_t) + 100}$$

where $MRPT_t$ is the mean repeatability for trait t , and K_t is the ratio of residual to sire variance for trait t . The mean number of effective daughters was assumed to be equal to 100, similar to the actual situation for young sires in Israel.

CR_t is dependant only on IS , h , a and G , and I and h will be constant for all traits. Thus, although IS was chosen arbitrarily, and h was computed for an arbitrary number of daughters, the relative values of CR_t will not differ. The following two indices were compared:

$$\text{INDEX1} = .51(\text{kg milk}) + 14(\text{kg fat})$$

$$\text{INDEX2} = .51(\text{kg milk}) + 14(\text{kg fat}) + 20(\% \text{ CS})$$

INDEX1 is proportional to the US PD\$. With the coefficients given, a kg of 3.5% milk will have a value of unity. Therefore if the profit from an additional kg of 3.5% milk is \$.1, then an increase of CS of 1% is assumed to have a value of \$2.0.

Expected correlated responses of milk, fat, and CS to selection by INDEX1 and INDEX2 are presented in Table 35. Accuracy is slightly lower for INDEX2, due to the lower MRPT for CS, as compared to the production traits. Although response for milk and fat are lower by 8% and 9% in INDEX2, which gives an economic weight for CS, progress for CS will be 5.1%. If an economic value of zero is assumed for CS, then the genetic decline for this trait will be .52. However, even if fertility is not included in the selection index, there may still be positive selection for fertility, due to culling of cows for nonconception. The correlated responses listed in this table were computed for two generations of sire selection, which is roughly equal to twelve years. Although less than the values presented in Table 26, the expected responses are similar to estimates of genetic trends for this population estimated above.

Table 35. Expected correlated responses of component traits and accuracies of sire evaluations for two selection indices.

	Traits	INDEX1	INDEX2
Economic weights	Milk (kg)	.51	.51
	Fat (kg)	14.00	14.00
	Conception status (%)	0.	20.00
Correlated response	Milk (kg)	1175.29	1090.92
	Fat (kg)	27.69	25.46
	Conception status (%)	-.52	5.10
Accuracy of index		.88	.86

Expected response after two generations of selection to changes in the economic weights for production traits (kg milk, fat and protein) were estimated by Ezra, Raz, and Weller (1988). Expected response for protein production varied from 18.1 kg in the current system (no price differential for protein) to 23 kg for direct selection on protein. Under the current pricing system, the expected genetic reduction in the sum of protein and fat percent is .21%. Under the Dutch pricing system (a negative price for fluid milk), the sum of protein and fat percent would increase by .05%. The expected ratio of fat to protein production varied from .94 in the current system to .98 for selection directly on protein.

Balcerzak, Freeman, and Willham (1989) estimated the effects of selection in the US dairy population for the direct and maternal components of dystocia for first, second-and-later, and all parities. The effect of restricting maternal change to zero and the effect of selection for only the direct component were also examined. Gene flow

procedures were used to compute economic weights as 1 and .347 for the direct and maternal effects, respectively. Genetic gain in aggregate genotype was the largest for first parity. For all parities, all the gain in the aggregate genotype was accounted for by the direct effects. At the same time, a slight decrease in the genetic maternal effects was observed. For all cases, there was almost no loss in aggregate genotype or accuracy when maternal changes were restricted to zero, vs. selection for both traits. Total genetic gain and genetic gain for the direct effect of dystocia both were greater, and accuracy of selection was lower when selection was only for the genetic direct effect, vs. the original index. Selection for only the direct effects is not likely to produce any significant change in dystocia as a maternal trait.

F. COOPERATION

Communication between the Iowa State University and the Agricultural Research Organization was greatly facilitated by the computer network BITNET. Dr. Freeman aided in the procurement of semen from elite US sires used the international elite sire comparison carried out in Israel. On his recommendation valuable genetic material was provided gratis by US AI institutes. Dr. Weller met with the US investigators at the Annual Dairy Science meetings in 1986 and 1988 in Davis, CA, and in Edmonton, AL; and at the 1988 Midwest Animal Science Meeting in Des Moines, Iowa. Dr. Ron attended the 1986 meeting on the genetics of disease resistance at Ames, Iowa, organized by the US scientists. Both the US and Israeli investigators attended the Third World Congress on Genetics Applied to Livestock Production in 1986 at Lincoln, NE. Dr. Ron presented the preliminary results of the five strain comparison at this meeting. The suggestions of Dr. Freeman and Berger were incorporated into the publication of these results. The multitrait REML variance component estimation program developed at Iowa State University was made available to the Israeli staff, and will be used routinely in the future.

G. MAIN ACHIEVEMENTS OF THE RESEARCH

The comparison of elite sires of five national strains under conditions of intensive management added substantial information to the previous comparison in Poland. Although only 5-6 sires were compared, and these sires were not a random sample for production traits, differences between these strains were greater under conditions of intensive management. Significant between strain differences were found for all traits studied. There was a strong genotype x environmental interaction only for the New Zealand strain. This information is being used for genetic comparison between these countries, and for decisions on semen purchase.

Dairy sire and cow evaluation procedures have been enhanced by incorporating new methodology. Programs were written to estimate BLUP sire evaluations for production, fertility, calving, and growth traits, and for mastitis susceptibility and cow survival. These programs are now part of the standard Israeli sire evaluation program. Since 1988 Israeli sires are routinely evaluated for protein production. Procedures to select bull dams in Israel have been improved, based on the results of this project. The threshold model procedure for analysis of calving ease data was presented to the Sire Evaluation Committee of the (US) National Association of Animal Breeders. This procedure was adopted as the basis of a national calving ease sire evaluations. Holstein sires are now routinely evaluated for ease of birth of their progeny in both Israel and the

US. Since 1970, most Israeli heifers have been bred to bulls with positive evaluations for calving traits. This procedure is being adapted to the US industry.

A program for multiple trait REML variance component estimation was developed and evaluated in the US under a "worst" case scenario: 1) all cows had 305d ME milk yield and number of services; 2) 68.4% of the cows were missing number of services as heifers; 3) heritability for number of services in cows and heifers was near or at the limits of the parameter space. Parameter estimates changed by accounting for missing traits: 1) heritability increased for 305d ME milk yield and decreased for number of services in heifers and cows, and 2) all genetic correlations decreased. A genetic antagonism between fertility and production was found for lactating cows of the US Holstein population. Sire analysts in the US are now reluctant to contract cows as bull mothers if they have long days open. The shortcut algorithm saved time and reduced computing expenses over both expectation maximization algorithms.

Methods were developed in both countries to adjust production records for past reproductive performance. Methods were also developed to adjust records of Israeli Holsteins for calving age and month, and to predict total production from incomplete lactations. Genetic evaluations computed from adjusted records were slightly more accurate than non-adjusted records. The adjustment factors developed in Israel were incorporated into the standard sire and cow evaluation procedures. The adjustment for days open developed in the US will

likely be incorporated in the animal model used to evaluate dairy cattle in the US.

Methods to account for heterogenous variance components among herds were developed in Israel and the US. This problem is probably not important for sire evaluation in Israel, because all sires are evaluated over many herds. It may be of major significance for evaluation of US sires, and bull dams in both countries. Data from herds all over the US were used to investigate the problem. Log transformations of the records produced evaluations that were more biased than evaluations on the untransformed records. Data were divided into three production groups by mean herd level. REML estimates of additive variance, permanent environmental variance, and residual variance, showed that the log transformation essentially stabilized the genetic variance, but not the other variance components. These can be easily stabilized in the residual variance matrix of the mixed-model equations. The correlations among sire evaluations computed from nonadjusted records and records adjusted for heterogenous variance were close to unity. However, the ranks changed substantially for elite sires and particularly cows. Adjustments for heterogenous variance should reduce biases due to different variances within herds. This procedure will be incorporated in the US animal model evaluation when appropriate parameters are estimated from the complete dairy population.

Genetic differences in health traits were estimated for both the US and Israel. US data of health-related incidences, recorded by

dairy producers as they occurred, and data copied from existing records were analyzed. The data recorded by producers were more reliable. Health traits were genetically correlated among mammary, digestive, locomotive, and respiratory systems. Reproductive problems were less related to other health problems. Heritabilities were large enough to indicate sires in AI could be ranked on health problems in their daughters, provided that nearly complete health incidences were recorded. This work has stimulated considerable interest from producers. The results of the genetic analysis of reproductive diseases in Israel were presented to the industry. Although the data set was more reliable than most previous set analyzed, heritabilities for all disease traits were still low. The preliminary results on the relationship between bacterial infection and somatic cell counts have been presented to the industry, and will serve as the basis for a more extensive Israeli study.

Data from the research herd for estimated feed efficiency from production records and feed consumption, demonstrated that smaller cows with lower body weights were more efficient producers. Also, phenotypic correlations of dams' body weight and measurements were positively associated with calf weight and negatively correlated with calving assistance. Smaller cows are more efficient, but have more calving problems.

Type traits have been studied extensively to identify those traits which singly or in combination with other traits are associated with increased productivity and longer herd life. Analysis of linear

type data showed that udder scores, stature, and dairyness were positively associated with production. The largest association with herd life was extreme dairyness and udder depth. Most traits were linearly associated with production, but had intermediate optima for herd life. For the latter, stature and udder depth had intermediate optima. Interest has been expressed in the US in using the combination of traits described by the first eight principal components of the factor analysis of conformation traits to report to dairymen, vs. all traits, to simplify interpreting the type results for sire progeny groups.

Phenotypic, genetic, and environmental trends in Israel for production and reproductive were estimated. Genetic trends were economically positive for all traits studied, except fat percent and days to first breeding. Prediction of future trends based of different selection goals have been presented to the Israeli dairy industry. Selection for direct and maternal effects for calving ease in the US population were evaluated using a combination of selection index and gene flow procedures. When selection is on first parity or all parities, nearly all gain in the aggregate genotype was for the direct effect. There is currently very little selection against dystocia in the AI population of the US. Current selection practices will not change the maternal effect. Increased selection for the direct effect may cause a negative genetic trend for the maternal effect.

Methods were developed to optimize the Israeli breeding program. It was found that genetic progress could be increased if more young sires were tested each year, and if a larger percentage of cows were mated to young sires. MOET for bull dams in Israel should increase genetic progress by 6-7 kg per year, and will reach the economic break-even point in about 15 years.

As work progressed under this BARD project, major problems were solved and new problems more clearly defined and solved. Solution to the problems addressed under this BARD project has already been and will be of tremendous value to the US and Israeli Dairy Industries. We feel this project has been very successful.

H. PUBLICATIONS

Note: * indicates 3 reprints are enclosed

1. Papers in reviewed journals.

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