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Estimation of Genetic Parameters for Production and Reproduction in Finnish Ayrshire Cattle

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ABSTRACT

Records of AI-sired cows born between 1978 and 1982 were used to form two composite production and reproduction data sets. First (second) consisted of 35,568 (26,443) first lactations of daughters of 270 (237) sires. Traits were FCM, heifer, and first parity nonreturn rates, days between calving and first insemination, and days open, with means 5075 (5280) kg, .62 (.62), .44 (.49), 81 (81) d and 110 (111) d. (Co)variance components were estimated by REML with an expectation maximization algorithm. Sire model included age, month, herd-year effects, and relationships among sires. Records on animals with observations missing on some traits were included. Estimates of heritabilities, averaged over data sets, were nonreturn rates for heifers and for cows, .02; FCM, .32; days to first insemination, .19; and days open, .10. Genetic correlations between first parity fertility and yield were unfavorable; the highest, .43, was between FCM and days open. Heifer nonreturn rate had a .09 correlation with production and a .26 correlation with cow nonreturn rate. Phenotypic correlations were in the same direction as genetic correlations but were smaller in magnitude. Results suggest that selection only for production would cause deterioration in level of fertility. When economical, AI sires should be evaluated for daughter fertility. A mul-

ti-trait model including milk production, days open and relationships among bulls is recommended for genetic evaluation.

INTRODUCTION

Reproductive problems cause economic losses for dairy farmers in many ways. Prolonged calving intervals decrease production per cow when measured by day of life. Infertility results in fewer calves born per cow per year and increased culling. These two factors together increase replacement costs and also reduce potential genetic gain due to selection for milk production. In Finland, only 12.6% of disposals were reported to be because of low production but 26.8% were because of reproductive failure (3). Another loss due to involuntary culling comes from the increased replacement rate that results in younger age structure in herds, thus lowering the actual production per cow.

Infertility contributes to increased breeding and veterinary costs. According to health control statistics, 33.8% of all veterinary treatments in Finland were because of infertility, and an average 22.8% of the cows in the health control program were treated for reproductive problems (12). Low breeding efficiency also increases labor costs. Herd management suffers because calving seasons or first calving ages might not be optimum economically.

High milk production has long been known to be associated with poor fertility, either because of genetic or environmental reasons (2, 6, 7, 8, 10, 15, 19, 23, 26). The same studies, however, have shown that heritability of breeding efficiency is generally below .05. Conclusions based on studies of reproductive genetics have been diverse and not always directly related to the results obtained. Some authors have concluded that due to low heritability, selection for higher fertility would not have much to offer (6, 11); others have concluded that despite low heritability, AI sires should be evaluated

Received September 16, 1988.

Accepted December 21, 1988.

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TABLE 1. Means and frequencies of milk, fat, protein and fat-corrected milk (FCM) yields in first five lactations of Finnish Ayrshire cows born 1978 to 1982.

Lactation number	Relative frequency	Milk	Fat	Protein	FCM
				(kg)	
1	.42	4904	217	160	5217
2	.28	5478	243	182	5836
3	.16	5867	260	193	6247
4	.08	5916	261	193	6281
5	.03	5941	261	194	6291
Total over all lactations	645,402	5343	237	176	5692

for reproductive efficiency and that some selection could be based on such evaluations to inhibit the decline in fertility resulting from correlated response due to selection for higher production (14, 18, 23, 25).

In Scandinavian countries dairy sires have been evaluated routinely for fertility of their daughters (21). In Finland, the evaluation has been based jointly on calving interval and number of services per conception in first three lactations and in Denmark on 56-day nonreturn rate to service for heifers and first lactation cows. In Norway, progeny tests are calculated for 60-d nonreturn rates for heifers and in Sweden for number of services per insemination period for heifers and for first parity cows separately, which are then combined in a single selection index.

The whole reproductive complex includes the events from birth to conception with successful parturition and postnatal survival of the calf. After first calving, good reproduction is characterized by a sequence of successive normal calvings with viable calves. The definition of female fertility used in the present study is strictly related to capability of the cow to conceive, including both the probability of successful service and the length of the period from calving to the new conception.

The objectives of this study were to estimate heritabilities of several measures of female fertility in Finnish Ayrshire cattle and correlations, genetic and phenotypic, among reproductive traits and between production and fertility. The goals were to determine the usefulness of these traits in sire evaluation and to compare estimates calculated by REML with estimates in the literature.

MATERIALS AND METHODS

The material was obtained from the Finnish Milk Recording agency and from Central Association of AI Societies. The records used were those of cows born between 1978 and 1982. Data were collected through 1978 to 1985, allowing some cows to have up to five normal lactations; however, only first lactations were analyzed. Total number of cows with milk production was 322,605 with 645,402 lactation records. Records of all AI of these animals were matched from AI registers. The two files were merged to form a composite data set of production and reproduction records. Due to Finnish Milk Recording procedures, only heifers that calve at least once enter the cow register. Therefore, only heifers with inseminations followed by calving were recorded in the data. Also, if a cow had no record of inseminations as a heifer, her records were deleted.

Measures of production were 305-d complete, uncorrected, twice daily milking, milk yields. If a cow had not finished 305 d in lactation, her production record was reported

TABLE 2. Overall reproductive level in first four lactations of Finnish Ayrshire cows born 1978 to 1982.

Lactation	Number of services per service period	Nonreturn rate after the first service	Number of first services
0	1.61	.62	200,115
1	1.90	.51	163,699
2	1.81	.54	129,646
3	1.77	.55	77,732
4	1.75	.56	39,263
Total	1.77	.56	635,678

TABLE 3. Number of records, sires, and herd-years in data sets used for variance component estimation.

Number	Data set 1	Data set 2
Records	35,568	26,443
Sires	270	237
Herd years for:		
Heifer services	12,618	8,884
Cow services	16,604	10,551
Production records	15,274	9,925

missing. Milk and fat yields were converted to 4% FCM yields. Number of services per service period was defined as the number of inseminations for a given cow in one lactation. If, however, there were more than 120 d between consecutive services, the later insemination was counted as initiating a different service period. Nonreturn rate (NRR) from the first service was computed by dividing the number of animals with one service by the number of service periods, i.e., first services. Calculated NRR equals to so called 120-d NRR, which is less than the 60-d NRR. The 60-d NRR is commonly used as a general measure of AI performance because it is less affected by early abortions. Tables 1 and 2 list the means and frequencies of production and reproduction records in the first five lactations. Because of the way the data were selected, the relative number of first lactations was greater than in the original population. Thus, overall means do not necessarily represent means in the population. Average age of heifers at first insemination was 480 d (standard deviation, 67 d) and at first calving 779 d (78 d).

Traits chosen for variance component estimation were: NRR from first insemination of heifers (NRR-H) and of first lactation cows (NRR-C), days from calving to first insemination (DFI), days open (DO), and FCM. Measurements of DFI, DO, and FCM were from the first lactation. To improve numerical stability, observations were standardized by dividing them by their approximate standard deviations; 20, 30, and 500 for DFI, DO, and FCM, respectively.

For variance component estimation, the data set was divided into two sets by heifer service year. The first set consisted of animals first inseminated from June 1980 through May

TABLE 4. Means and standard deviations of reproductive traits and fat-corrected milk production in data sets used for variance component estimation.

Trait	Data set 1		Data set 2	
	\bar{X}	SD	\bar{X}	SD
Nonreturn rate, heifers	.62	.48	.62	.48
Nonreturn rate, cows	.49	.50	.49	.50
Days to first insemination	81	28	81	28
Days open	110	49	111	50
Fat-corrected milk, kg	5075	923	5280	913

1982. The second set included heifers inseminated from June 1982 through May 1984. Animals born after their sires had their first progeny test evaluations were excluded. Every sire was required to have at least 75 daughters. Records of daughters of other sires were discarded. Next, records of animals that belonged to NRR-H comparison groups with no contemporaries were removed. After repeating the procedure a second time, the reductions in the data set were small enough to suggest that selected animals were daughters of sires with at least 70 to 75 daughters in herd-years with at least one herd mate. Table 3 shows number of records, sires, and herd-years in each data set. Table 4 lists means and standard deviations of FCM yield and measures of reproduction in the samples.

The following general multivariate model described the records:

$$y = X\beta + Zu + e$$

where y is a vector of observations, recorded or missing, of t traits on n cows. β is a vector of unknown fixed effects including herd-year, age, and month effects for each trait. Ages were classified in 12 classes: for first service age in heifers the first class included ages 300 to 390 d, followed by classes of length 30 d up to last class 690 to 800 d; for cow first service age the first class was ages less than 767 d, class length 35 d; for calving age the first age class included cows freshening at 590 to 660 d, class length 35 d, and last class 1010 to 1150 d. u is an unknown vector of random sire values ordered

TABLE 5. Estimates of phenotypic standard deviations, heritabilities,¹ and genetic² and phenotypic³ correlations for nonreturn rate of heifers (NRR-H), nonreturn rate of cows (NRR-C), days from calving to first insemination (DFI), and 4% FCM yield (FCM) from both data sets (35,568 and 26,443 Ayrshire cows).

Trait and data set	SD	NRR-H	NRR-C	DFI	FCM
NRR-H					
1	.476	.02	.22	.27	.14
2	.474	.03	.31	.40	.03
NRR-C					
1	.490	.03	.02	.09	-.23
2	.487	.04	.02	-.29	-.29
DFI ⁴					
1	24.45	.07	.02	.13	.31
2	24.53	.08	.03	.23	.15
FCM ⁴					
1	668.3	-.04	-.21	.16	.35
2	667.3	-.03	-.21	.14	.28

¹Heritabilities are diagonal elements.

²Genetic correlations are above diagonal.

³Phenotypic correlations are below diagonal.

⁴Units for DFI are days; for FCM, kilograms.

by traits within sires, so that $\mathbf{u}' = (\mathbf{u}_1' : \mathbf{u}_2' : \mathbf{u}_3' : \dots : \mathbf{u}_q')$, with \mathbf{u}_i being a vector of transmitting abilities of t traits of the i th sire, \mathbf{X} and \mathbf{Z} are known incidence matrices, and \mathbf{e} is a vector of random residual effects.

Culling pattern in the data was mostly sequential in order of NRR-H, NRR-C, DFI, DO and FCM. To avoid possible bias due to the selected data (30, 32), observations with sequential trait combinations starting with NRR-H were utilized. When an animal was missing data for any of the traits, the missing observations were replaced with a dummy value of 0 and nulls were substituted for corresponding rows of \mathbf{X} and \mathbf{Z} . This procedure has no effect on solutions but does simplify the notation used.

Further, the random effects were assumed to have the following distribution:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \end{bmatrix} \sim \text{MVN} \left\{ \begin{bmatrix} \mathbf{X}\beta \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{V} & \mathbf{ZG} \\ \mathbf{GZ}' & \mathbf{G} \end{bmatrix} \right\}$$

where $\mathbf{V} = \mathbf{ZGZ}' + \mathbf{R}$, $\mathbf{G} = \mathbf{A} \otimes \mathbf{G}_0$, with \mathbf{G}_0 the $t \times t$ matrix representing sire variance, one-fourth of the additive genetic variance-covariance matrix of the traits, and \mathbf{A} , the numerator relationship matrix for sires. The \otimes symbol denotes the direct product operator. $\mathbf{R} = \text{Diag}\{\mathbf{R}_i\}$, $i = 1, \dots, n$, where \mathbf{R}_i is $t \times t$ variance-covariance matrix of residuals for i th

animal. Let \mathbf{R}_0 represent variance-covariance matrix of an animal with all traits recorded, then each \mathbf{R}_i can be formed from \mathbf{R}_0 by replacing rows and columns corresponding to missing traits by zeros.

Variance-covariance matrices, \mathbf{G}_0 and \mathbf{R}_0 , were estimated using the method of restricted maximum likelihood (22). The REML solutions were iterated using expectation maximization-like algorithm (4), as described by Mäntysaari (20). At each round of iteration the nonlinear maximization step for residual variance components was not subiterated completely but the first round solutions of successive approximation were used instead. For sire variance components the maximization step is linear and was solved normally. Starting values for iteration for data set 1 were obtained using Henderson's method 3 (13) for variances; for covariances, zeros were used. For data set 2, estimates from data set 1 were used as starting values.

RESULTS AND DISCUSSION

Table 5 shows the estimates of heritabilities and genetic and phenotypic correlations obtained from both data sets for heifer NRR, cow NRR, DFI, and FCM. Estimates were calculated with the corresponding first service months and ages in the models of NRR-H and

TABLE 6. Estimates of phenotypic standard deviations, heritabilities,¹ and genetic² and phenotypic³ correlations for nonreturn rate of cows (NRR-C), days from calving to first insemination (DFI), days open (DO), and 4% FCM yield from both data sets (35,568 and 26,443 Ayrshire cows).

Trait and data set	SD	NRR-C	DFI	DO	FCM
NRR-C					
1	.490	.02	-.07	-.55	-.24
2	.488	.02	-.65	-.89	-.24
DFI					
1	24.46	.03	.13	.84	.35
2	24.72	.03	.30	.92	.20
DO ⁴					
1	45.69	-.61	.47	.05	.55
2	46.99	-.60	.47	.15	.29
FCM ⁴					
1	665.1	-.20	.18	.30	.36
2	665.7	-.20	.15	.28	.28

¹Heritabilities are diagonal elements.

²Genetic correlations are above diagonal.

³Phenotypic correlations are below diagonal.

⁴Units for DFI, DO are days; for FCM, kilograms.

NRR-C and calving months and ages in the models of DFI and FCM. Data set 1 was iterated 32 rounds, and number of iterations in data set 2 was 30. At that stage average absolute changes in standardized sire variance-covariance components per round were .00003 and .00002 for data sets 1 and 2, respectively. Convergence of residual variances was much better than the convergence of sire variances. Therefore, for analyses that are discussed later, convergence was assumed when the average absolute round-to-round change in standardized sire (co)variance components was less than .0002. However, each analysis was iterated a minimum of 23 rounds, resulting in even greater convergence for some estimates.

Table 6 shows the estimates of heritabilities and genetic and phenotypic correlations for the analysis after NRR-H was replaced by days open. The model for DO was the same as for DFI, including herd-year, calving month, and age effects.

Phenotypic standard deviations and correlations were similar for both data sets. Heritabilities and genetic correlations, however, were more variable (Tables 5 and 6). Heritabilities of fertility traits were larger in the second data set, whereas heritability of production was larger in the first data set. The magnitude of the differences between the data sets can hardly be explained by random sampling. A possible expla-

nation for divergency is that the first set of sires included 41 sons of two imported bull sires. In the second set, there were no direct descendants of these two sires. Sons of the imported bulls had the three best rankings in sire solutions for FCM, with PD of 577, 494, and 492 kg, which equal 3.3, 2.8, and 2.8 in units of sire SD. In data set 2, the best bulls had PD of 443, 400, and 377 kg, although due to the smaller sire SD, their relative proofs were similar to those in the first set. Thus, heritability of FCM in the first data set may be somewhat higher because of the introduction of new genetic variation by imported bulls sires. The reason for higher heritabilities of reproductive traits in the second data set is unknown but might be due to sampling variance for traits with small heritability.

Variability in estimates from the same data set but with two different models (Tables 5 and 6) may result from different relationships between production and fertility. In the first data set genetic correlations of DFI and DO with FCM were much higher than in the second set. When DO was included in the model DFI behaved similarly as DO, so that the correlation between NRR-C and DFI decreased.

Heritabilities

Heritabilities of NRR were about .02, which agree with other studies (16, 18, 19, 25). For

interval traits, DFI and DO, the estimates were larger than usually found in the literature. Estimates averaged over data sets and different analyses were .10 for DO and .19 for DFI when individual estimates were averaged by weighting by the number of sires in data sets. In other studies where both DFI and DO have been included, heritability of DFI is commonly found to be larger than that of DO, with estimates averaging about .04 and .02 for DFI and DO, respectively (2, 10, 17, 18). Schneeberger and Hagger (26) found heritability to be .09 for DFI, twice that for DO, which was .04. Hermas et al. (14) found even greater difference. Their estimate for heritability of DFI was .13 and for DO only .04. None of these studies incorporated the relationship matrix among sires into the model. In studies where data have been analyzed both with and without A^{-1} (31), or with different levels of completeness of relationships (5), larger heritabilities have been found with more relationships in the model.

A simulation study by Sorensen and Kennedy (28) showed that in a random mating population variance component estimates of additive genetic variance are biased downward if relationships are ignored. When selection had been practiced for several generations, Henderson's method 3, even with relationships incorporated in expectations, was not able to provide unbiased estimates, whereas univariate minimum variance quadratic unbiased estimation [MIVQUE, by Rao (24)] gave unbiased results even in a case of selection. They argued that the reason was because when A^{-1} is used with the animal model, MIVQUE and REML are "sufficient estimators", since they make use of all available information. With fertility data, records used probably result from long-term selection against sterility. Thus, estimates not based on the ML approach and complete relationships may be biased downward. More research is needed to find out if these biases are smaller or greater when heritability is low.

Thompson (30) suggested that multivariate methods based on likelihood estimators will yield estimates unbiased by selection on one of the traits if all the information is included in the analysis. Walter and Mao (32) compared multi-trait and single-trait REML estimates of variance components in simulated populations. When selection mimicking sequential culling between lactations was practiced on first of the

TABLE 7. Single-trait estimates of heritabilities (h^2) and phenotypic standard deviations for nonreturn rate for cows (NRR-C), days to first insemination (DFI), days open (DO), and 4% FCM (35,568 and 26,443 Ayrshire cows).

Trait	Data set 1		Data set 2	
	SD ¹	h^2	SD	h^2
NRR-C	.490	.02	.487	.02
DFI	24.48	.15	24.76	.31
DO	44.84	.04	45.98	.08
FCM	662.7	.35	664.6	.28

¹Units for DFI and DO are days; for FCM, kilograms.

two correlated traits, the single-trait estimate of heritability of the second variable was reduced. Selection had no clear effect on multi-trait REML estimates.

To compare multi-trait estimates with single-trait estimates of variance components, analyses were carried out while forcing all covariances to be zero after each round of iteration. The average single-trait estimate for heritability of DO was .06 (Table 7), which was smaller than the estimate with the same model but taking into account the correlations to other traits. Thus, it may be that usual estimates of heritability of DO are biased downward because of selection on milk production. For DFI, however, ignoring correlations had an adverse effect, suggesting that the high estimate of heritability needs to be explained by reasons other than selection on correlated traits.

To examine whether estimates were sensitive to changes in the model, data also were analyzed with a model where fixed effects in the models of DFI and DO were the ones in the model of NRR-C, i.e., first service months and service ages (Table 8). Heritabilities of both traits, especially DFI, decreased to the level typical for other studies. Most studies with fertility traits have been done with a simple sire and herd-year-season effects model (2, 10) or models with a regression to the average herd production level (8) or to reproduction level (18). Thus, a possible reason for higher heritabilities found in the present study was that a more complete model was used.

Genetic Correlations

Genetic correlations among fertility traits were mostly favorable; the general level of fer-

TABLE 8. Estimates¹ of phenotypic standard deviations² and heritabilities (h^2) for nonreturn rate of cows (NRR-C), days from calving to first insemination (DFI), days open (DO), and 4% FCM yield from both data sets, with service age and month in the model of DFI and DO (35,568 and 26,443 Ayrshire cows).

Trait	Data set 1		Data set 2	
	SD	h^2	SD	h^2
NRR-C	.490	.02	.487	.02
DFI	22.73	.03	22.51	.05
DO	44.85	.03	45.68	.04
FCM	665.8	.36	665.5	.27

¹The REML estimates with multi-trait model.

²Units for DFI and DO are days; for FCM, kilograms.

tility seems to be partly regulated by the same physiological factors. Heifer NRR had a moderate genetic correlation with cow NRR (.22 to .31) and with DFI (.22 to .40). Results agree with most previous studies. Hansen et al. (11) reported .20 to .42 for correlation between number of services for heifers and for first parity cows. Ron et al. (25) calculated correlation of sire PD for heifer NRR and cow NRR to be .27. Some authors have, however, reported that these two traits are essentially the same (18). In the second data set the correlation between cow NRR and DFI was high, -.29 to -.65, but estimates from first data set were inconsistent. Standard errors of estimates of genetic correlations for traits with low heritability might be large. The expectation maximization algorithm does not provide SE of estimates.

The genetic correlations indicate an antagonistic relationship between production and reproduction in the first lactation, and a slight but favorable relationship between heifer reproduction and milk production. Although correlation between NRR-H and FCM was .14 in the first set, it was .03 in the other set. These estimates support Hansen et al. (11), who also found evidence of small favorable genetic relationships between heifer fertility and production capacity. The estimate of genetic correlation between production and NRR at first parity was -.25, when it was calculated as a weighted average over both data sets. Similarly, average genetic correlation between DFI and FCM was .26. It has been argued that the stress due to production and a negative energy balance in

early lactation are responsible for reduced fertility in high producing animals. These mechanisms have been studied extensively, but no definite physiological explanation for the relationship has been found. There seems to be more evidence that energy status and milk production would affect the reappearance of estrous cycles and strength of signs of estrus, and therefore opportunities for early first service, than they would affect conception rates (7, 33). The fact that genetic correlation between fertility and production is larger than the phenotypic correlation may complicate physiological studies. Even if, in general, high production is associated with problems in reproduction, the phenotypic variation among animals will make the observed relationship small and difficult to detect in experiments.

The estimate of genetic correlation between DO and FCM averaged .43, being considerably larger than the average of those between production and DFI or NRR. An obvious explanation is the competition for nutrients between growing fetus and mammary gland at late lactation. The long interval between parturition and first service or failure to conceive from the first service also will cause prolonged calving interval and so will affect milk production during later stages of lactation. If short (60 to 120 d) production records are used, the direct effect of conception on milk yield can be eliminated. Berger et al. (2) found the relative increase in genetic correlation with production was about same for DFI and DO when 120-d production was changed to 305-d yield. Hansen et al. (10) found the correlation between DFI and 120-d production to be higher, although insignificantly, than the one with 305-d production. Hence, the genetic correlation between milk yield and DO is larger than the correlation between production and DFI despite the production measure used and is not necessarily due to decrease in production in later stages of lactation caused by the pregnancy. Days open is a function of DFI and NRR, which both have negative correlation with production; thus, a large antagonistic relationship between DO and FCM might reflect the increased accuracy of that measure of the general level of fertility.

Phenotypic Correlations

Phenotypic correlations generally were smaller than genetic correlations. Phenotypical-

ly, heifer fertility can be concluded to be neither connected to fertility at first lactation nor to first lactation production. This conclusion supports other findings (11, 17). Interesting, although not practically meaningful, is the phenotypic correlation between NRR-C and DFI in the second data set, which in sign is opposite to that of the genetic correlation. This phenomenon, also found by Janson (18), shows that the same animal-based factors that delay first service also cause lower conception rate after that service, but that those environmental factors that lead to longer intervals between calving and first service enhance the probability of successful service. If this phenotypic relationship (Table 6) is converted to linear regression, the regression shows that each additional 10 d in DFI will increase NRR-C by .50% units (data set 1) and .57% units (data set 2). Empirically this relationship is known to be nonlinear (2, 15, 25) with a negative quadratic coefficient.

All phenotypic correlations between reproduction and production were unfavorable. It has been suggested that farmers may deliberately breed high producing cows later than low producers, allowing them to have longer calving intervals. In first lactation data such practices should show as an inflated phenotypic correlation between DFI and FCM. However, the observed correlation was smaller than the genetic correlation, which indicates that preferential withholding of services is not common. Berger et al. (2) reached the same conclusion after examining the correlation between 60-d yield and first breeding interval.

Solutions for Age and Month Effects

Age and month solutions were computed relative to last category of each factor, which was set equal to zero. A marked difference between months in NRR was found (Figure 1). For both cows and heifers the best results in both data sets were obtained for insemination started in July, August, or September. The poorest results were recorded for February. Difference between the poorest and the best month in cow NRR was -17 . Seasonal patterns are related to climatological and management conditions. Most cows in Finland are housed in stanchion barns, except during the pasture period from June to September. Depression of

fertility during the indoor feeding season is clear. Increasing daylight in spring seems to be associated with improvement in conception rates. The best fertility is obtained on pasture, with a sharp drop in NRR at the beginning of indoor feeding. The pattern of seasonal changes is closely associated with geographical location. North American studies showed the highest conception rates in March (15). In Israel NRR were highest in December, January, February, and March (25). The pattern reported by Janson (18) from Sweden was almost identical to the one found in this study. Of interest in his estimates was the small increase in NRR from January to March followed by a decline for May; a similar pattern also is recognizable in Figure 1.

Figure 2 shows seasonal effects on interval traits, DFI and DO, plotted against calving month. These traits are more affected by management decisions than NRR. With the Finnish milk pricing policy it is advantageous for cows to calve in the fall. Some cooperative dairies also discount insemination costs to their members for cows inseminated to calve in the fall. In addition, fall freshening cows have the highest milk production (20). Therefore, it may be interpreted that the shorter DFI for cows calving September to January are caused somewhat by farmers' intentions to keep cows calving in the fall, whereas average DFI for July might be increased by deliberately delaying services to move expected calving to fall season. However, the shortest intervals to first service are with cows freshening in May, which indicate that pasture period has a positive effect on postpartum reproductive performance. Whether this effect is due to physiological or management reasons is unknown. Monthly changes in average DO are caused by variation in DFI and NRR. Although number of days to first breeding is high for cows calving in March, DO is average, because conception rates during summer, when most spring calvers are inseminated, are high. Seasonal variation in interval parameters is not well documented. Janson (18) modelled DFI and calving interval with first service months. He reported that in Sweden cows that are first inseminated in September and October have the shortest DFI and calving intervals. The highest intervals were observed with cows inseminated in April.

Within parity, the age of the animal does not seem to have significant effect on measures

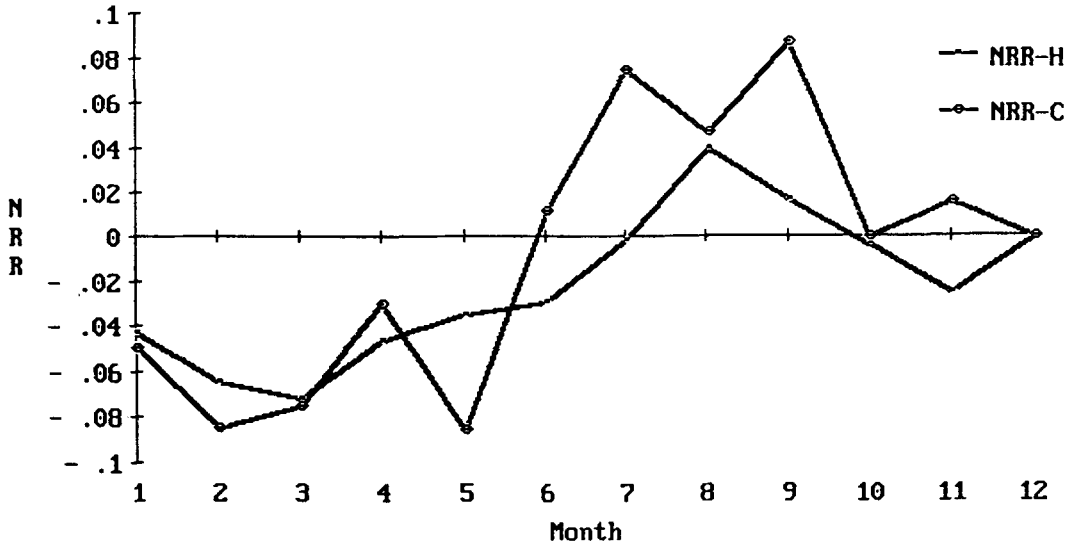


Figure 1. Generalized least squares solutions for effects of service months on heifer (NRR-H) and cow (NRR-C) nonreturn rates. Data set 1 with 35,568 Ayrshire cows.

of reproduction. This result agrees with other studies (9, 18). In Figure 3 are solutions for age effects for DFI from analyses with either calving or service age in the model. As calving age increases, DFI slightly decreases, but the effect of service age seems to be positive. When a cow has longer DFI she is likely to be older at

the time of service, which partly explains the later relationship. This phenotypic confounding, which increases the apparent coefficient of determination, or fit, of the model, can be verified from the smaller residual variances. This confounding, however, seems to have even greater effect on sire variance and thus reduces herita-

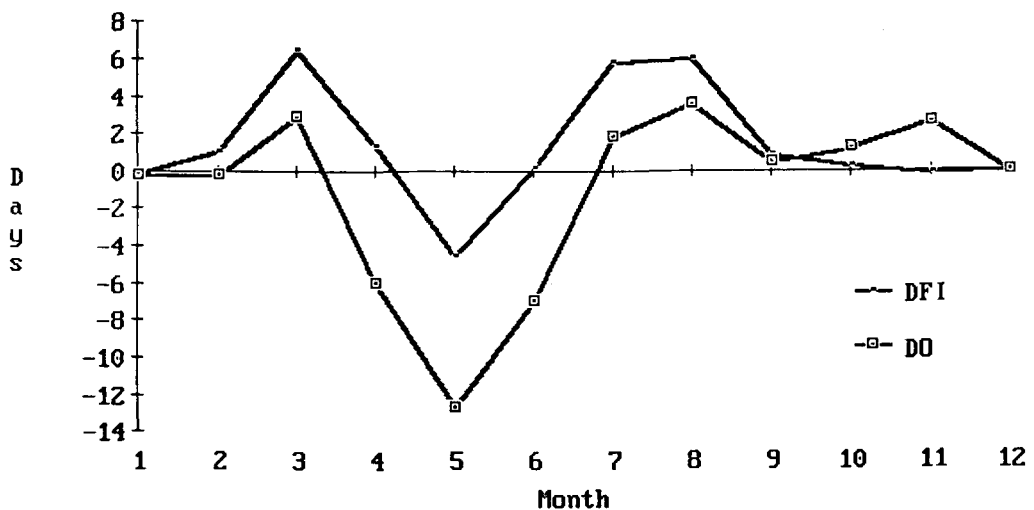


Figure 2. Generalized least squares solutions for effects of calving months on days to first service (DFI) and days open (DO). Data set 1 with 35,568 Ayrshire cows.

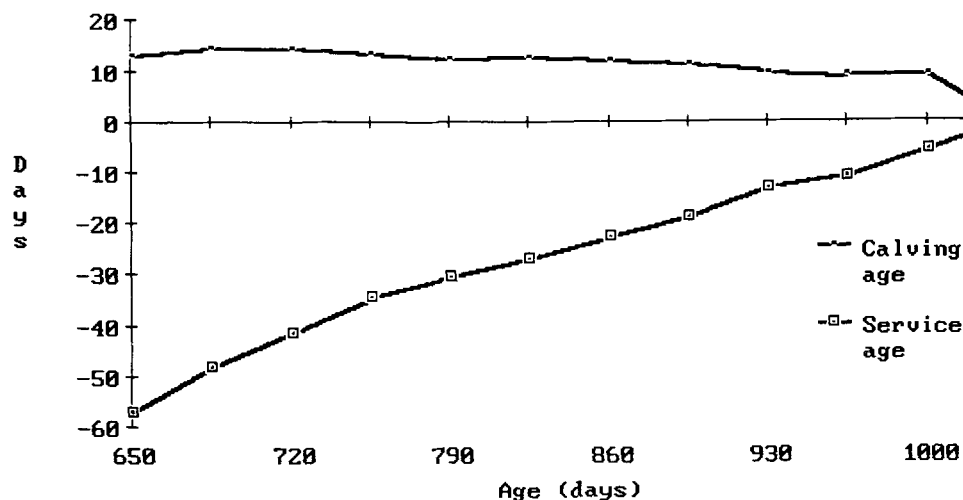


Figure 3. Generalized least squares solutions for age effects on days to first service from two different models. First model with calving age and month; second model with service age and month. Data set 1 with 35,568 Ayrshire cows.

bility estimates. A larger part of variability in DFI may be due to genetic effects: different rates of maturation as a heifer and differences in reconditioning after parturition. When that variability is removed by having age effects in the model, heritability estimates for DFI and DO are reduced.

Implications to Breeding Programs

The unfavorable genetic correlation between reproductive measures and production suggests that selection only for production would cause deterioration in general level of fertility. Based on parameter estimates presented in this study (additive genetic SD of 376 kg and 14.5 d for FCM and DO, and genetic correlation of .43; averages from both data sets), expected correlated response would be 1 additional d in DO/60-kg genetic increase in FCM. Little is known about the long-term economic consequences of this deterioration.

As a result of low heritability, genetic improvement or maintenance of fertility has to be based on progeny testing of AI sires. Crucial for successful selection is that the trait evaluated be as closely correlated as possible to the breeding objective. Heritability of selection criterion should be as high as possible, with a large phenotypic variance. Evaluations of the trait should be available early in the life of the

animal, preferably before production records are available. In addition, evaluation of the trait should be unbiased by selection or involuntary culling.

None of the traits considered in this study fulfill all criteria. Heifer NRR is available before any other reproduction traits, and it is not affected by selection or culling unless a high proportion of heifers is not inseminated because of lack of heat signs, i.e., are completely sterile. However, the heritability of heifer NRR is small, and the genetic correlation between heifer and cow fertility is of questionable magnitude. The NRR from first service as a cow suffers from low heritability, which may be caused by the discontinuity of the trait. It is not well understood under what conditions binary variables should be analyzed on observed scale and when categorical methods would be more effective. Problems with the trait in Finnish data might be related to extremely small subclass size.

Number of days to first insemination had the highest heritability of all reproductive traits in this study, is available also for animals without two calvings, and is fairly robust against selection or culling. For a long time DFI has been neglected in animal breeding work on the basis that most of its variation is caused by management. Insemination at less than 60 d following

calving has not been recommended because early breedings were assumed to have detrimental effects on the later reproductive performance of the animal. Short DFI also was known to result in low conception rate from the first service (27). Later studies showed that although starting to inseminate cows earlier in the lactation results in more services per conception, earlier breeding also leads to shorter calving to conception intervals (33). Studies also have shown that early postpartum breeding does not have any negative effects on other aspects of reproduction and that shortening DFI would be a recommended tool for shortening calving intervals (28, 33).

Both NRR and DFI are missing if cows in the first lactation are not inseminated. In addition, NRR can be biased if the cows poorest in production or heifer fertility are bred only once despite the result of the service.

Advantage of days open as a selection criterion is that DO is directly related to the most important reproductive trait, calving interval. In this study heritability of DO was estimated to be low, .10, although higher than in most studies. If DO is predicted from last insemination day, it is available rather early in an animal's life, before first parity production information. Generally the DO measure is missing if DFI or NRR records are missing. Also cows that are culled during their first lactation will not usually have DO records. Although predicted DO might be accurate for lactations in progress, predicted DO is subject to many errors when estimated from cows that have left herd before second calving. Disposed animals can be judged pregnant if they are not rebred in 120 d following last service, as was done in this study, but the method is only approximate and, for example, does not use information on cows that left herd, e.g., right after their, say, 10th service.

Selection of the trait or traits affects the choice of computational techniques to be used in the genetic evaluation. For low heritability traits, multi-trait methods with relationships incorporated are recommended. By utilizing production information, the accuracy of evaluation for fertility traits could be improved. Based on the estimated heritabilities and correlations the genetic merit of the sire would seem to be fairly well expressed in the evaluation of days open. Days open has high genetic correlations

with DFI and NRR and has greater economic value than either of them.

In many sire evaluation programs production records are corrected with respect to DO. The goal is to adjust milk yield for the effect of the stress caused by pregnancy. Therefore, knowing whether the animal conceived from service at d 200 of the lactation is not critical, since the cow was still open at 200 d postpartum, indicating that the pregnancy would have only a small effect on depressing production. In these "operational" DO records, animals that are not bred at all are classified in the same category as animals that are assumed to conceive late in the lactation. Also, because no attention is paid to whether disposed animals are pregnant or not, the left-herd day can be thought as a termination point of DO. In practice "operational" DO would be an ideal trait to use in evaluation of reproductive performance as it is a by-product from sire evaluations for production traits. It can be defined and measured accurately because it is not an estimate of the true DO but merely an artificial fertility measure correlated with it. Culling would not result in missing observations, although some error would be involved because low producing animals that disposed of rather than inseminated at the end of the lactation would be assumed also to have poor fertility. In sire evaluation programs where short lactation records are projected to full length, a small number of animals would have no information on DO. For them expected value, i.e., the average value of DO, could be substituted for "operational" DO.

Further simplification of computations is achieved by using "operational" DO records, which could be defined to exist for every production record. For pairs of traits with the same design matrices, multivariate analysis can be transformed into two separate single-trait evaluations by using canonical variates (1). More research, however, is needed before use of such artificial measures of reproduction, as "operational" DO, can be justified. Until then analyses that allow missing production or reproduction traits in records of individual animals is preferred.

ACKNOWLEDGMENTS

This research was conducted using the Cornell National Supercomputing Facility, a re-

source of the Center for Theory and Simulation in Science and Engineering at Cornell University, which is funded in part by the National Science Foundation, New York State, and the IBM Corporation.

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