## GENETICS AND BREEDING

# Genetic Parameters for Milk Yield, Survival, Workability, and Type Traits for Australian Dairy Cattle

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## ABSTRACT

Genetic parameters, such as heritabilities and genetic correlations were estimated for milk yield, survival, workability, and type traits for Australian Holstein-Friesian and Jersey cattle. All analyses were performed using multivariate REML with a sire model. Heritabilities for lactation yield traits were moderate, ranging from .20 to .28, and heritabilities for mean test day deviations were approximately .40 higher. Heritabilities for survival (probability of surviving to the next lactation) were low, ranging from .02 to .08. Genetic correlations between survival scores were high, ranging from .37 to .98, in particular between adjacent survival scores (on average .91 and .97 for Holstein-Friesians and Jerseys). Heritabilities for stayabilities were larger, ranging from .03 to .22. On average, genetic correlations between stayabilities were very high, ranging from .66 to .99. For milking speed, temperament, and likeability, heritability estimates ranged from .18 (for likeability in Holstein-Friesians) to .29 (for milking speed in Jerseys). Undesirable scores for milking speed and temperament had negative genetic correlations with stayabilities (correlations approximately –.20). Heritabilities for type traits were all moderate (.11 to .42), and genetic correlations among type traits and between type traits and production traits were large. Phenotypic correlations between type traits and stayabilities were low. Generally, genetic correlations between type traits and stayabilities were low although the standard errors of those estimates were large.

(**Key words**: genetic parameters, milk yield, stayability, workability, type traits)

**Abbreviation key**: **ABV** = Australian breeding value, **ADHIS** = Australian DHI scheme, **HF** = Holstein-Friesian, **J** = Jersey, **STAY$_i$** = stayability until lactation i.

## INTRODUCTION

During August 1994, a customized sire selection computer program (P. J. Bowman, P. M. Visscher, and M. E. Goddard, unpublished) was released in Australia. The program is based on an application of selection index theory (12) for which genetic parameters are needed, such as heritabilities and genetic correlations for traits in the breeding objective and traits in the selection index. Traits in the breeding objective have been defined previously (32). Traits in the index are a selection of the many Australian breeding values (**ABV**) that are calculated for dairy bulls in Australia. At present, the Australian DHI Scheme (**ADHIS**) publishes up to 40 ABV per bull (1): 5 ABV for yield traits (milk, fat, and protein yield and fat and protein contents), 3 ABV for workability (milking speed, temperament, and likeability), 30 type ABV, and ABV for survival and calving ease. The ABV for yield traits are predicted using BLUP with an animal model (13, 14). All other ABV are from BLUP evaluations using sire or sire-maternal-grandsire models. All ABV are from single-trait analyses.

Genetic parameters for many of the traits for which ABV are calculated have not been estimated recently from Australian data. Meyer (17) estimated genetic parameters for first and second lactation yield traits for Holstein-

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Friesian (HF) cattle with REML (22). Madgwick and Goddard (15) calculated estimates of heritability for survival traits with univariate REML. Meyer et al. (20) estimated parameters for test day milk and fat yields for HF cattle with REML. Heritabilities for type traits for HF data were estimated by Meyer et al. (19) and Smith (29). Genetic parameters for workability data for Australian dairy cattle have not been published previously, and estimates from other countries are rare and imprecise, in particular for temperament. For Australian Jersey (J) cattle, no recent documentation of genetic parameters exists for any trait.

For the ABV calculations for yield traits with an animal model, the traits analyzed are not the usual 305-d yields (or estimates thereof), but a function of test day deviations (13, 14). The reasoning behind the use of these deviations is that comparison of cows on the same test day should remove more environmental variation, in particular for production systems based on pasture. Although Meyer et al. (20) showed the advantage of using models based on test day data, the traits used in the ABV calculations were not analyzed directly.

One of the traits in the breeding objective of the sire selection program is survival from involuntary culling and death, which was defined as the observed survival of progeny of bulls adjusted for the breeding values of those progeny for milk yield and workability traits (Bowman, Visscher, and Goddard, 1994, unpublished). For young bulls for which daughters have not yet had the opportunity to provide survival information, type traits are possible predictors for survival or herd life (3, 7, 25, 28). For Australian data, Madgwick and Goddard (15) reported genetic correlations between survival traits and milking speed, temperament, and a single type trait (overall type). Only phenotypic relationships between survival and other traits have been documented elsewhere (2). Research in other countries has not produced reliable or consistent results for the genetic correlations among survival, yield, type, and workability.

The aims of this study were to estimate genetic parameters for yield traits, survival traits, workability traits, and type traits. In particular, the results provide new information on 1) the comparison between genetic parameters for HF and J cattle, 2) the heritabilities of yield traits calculated using test day deviations, 3) genetic parameters for workability traits, and 4) genetic correlations of survival traits with other traits.

## MATERIALS AND METHODS

### Data

Data on yield, workability, and type classification were provided by ADHIS. For the states of Victoria, New South Wales, Queensland, Western Australia, and South Australia, all yield records of cows calving for the first time from 1980 to 1992 were extracted subject to stringent edits. Cows were required to have yields for milk, fat, and protein recorded for all lactations. For herds that did not continuously participate in herd recording from 1980 to 1992, only those records from the earliest continuous period were used. A database was created with a herd, sire, and dam identifier, date of birth, and the number of recorded lactations for each cow. For each lactation, date of calving, lactation length, and total lactation yields for milk, fat, and protein were recorded, as was the average test day deviation for milk, fat, and protein yields. The average test day deviation is calculated by ADHIS prior to the national evaluation with an animal model (14) and is an average test day deviation from contemporaries (cows that had a test on the same day), corrected for age at calving and stage of lactation (13).

Workability traits consisted of milking speed, temperament, and likeability. Traits were scored by farmers on heifers with a five-point linear scale (the farmers scored on an A to E scale, but throughout the study we used a corresponding five-point numeric scale); a low score was desirable (i.e., high milking speed, good temperament, and high likeability). The score for likeability was the response to the question: all things being equal, would you like more cows like this one in your herd? (1, 2). Workability data were only retained for cows with records of yield.

Type data were classified by the Holstein-Friesian Association of Australia and the Australian Jersey Breeders Society. Only type data from progeny test herds (i.e., herds that participate in testing unproven bulls through an agreement with AI centers) were used in subsequent analyses because genetic parameters were expected to be different for commercial herds and herds with pedigree recording [e.g., (4, 5, 25)], but the interest for this study was in the relationship between survival and type traits in commercial herds. For example, the correlation between survival and some type traits may be larger in herds with pedigree recording because breeders in those herds cull cows based on their (bad) type scores. To reduce the amount of computation and output, a selection was made for further analyses of 13 out of 30 recorded type traits. The 13 traits were selected on their similarity to conformation traits that have shown relationships with herd life [e.g., (3, 7, 25, 28)] in other countries. Type traits were a mixture of summary traits, scored on an 18-point scale, and linear traits, scored on a 9-point scale. Type data were only retained for cows with records of yield.

Two measurements of length of herd life were used: survival scores and stayability. Survival i was defined as the probability of surviving in the herd from lactation i to lactation i + 1 (15). Survival was an all-or-none trait and was scored as 0 or 100%. If the last test day of the herd in the data file was <500 d after a cow calved to begin lactation i, then survival i was undefined because we could not ascertain whether the cow was still in the herd or had been culled. Cows were scored 100% for stayability until lactation i ($\mathrm{STAY_i}$) if they commenced lactation i and 0% otherwise. Cows were assumed to have had the opportunity to express $\mathrm{STAY_i}$ if date of last known calving + (i − k − 1) × 365 + 500 was before the date of the last known test of the herd, where k is the order number of the last known calving. Using this definition of stayability, $\mathrm{STAY_2}$ is equivalent to the probability of surviving in the herd from lactations 1 to 2, and $\mathrm{STAY_1}$ = 100%.

### Statistical Analyses

All analyses were performed with REML from a sire model. Sire models were used throughout because multiple-trait animal models with large data files still have prohibitively expensive computation costs. For all analyses, relationships among bulls through their sires were taken into account with a relationship matrix. The HF data had records of cows sired by an HF sire; records of cows sired by a J sire were in J data. Four different data files were analyzed for each of the two breeds. Summary statistics for all analyses are in Table 1.

*Analyses of Survival Scores.* No residual correlation existed between different survival scores because survival scores for lactation j were only defined for cows surviving all previous lactations. The REML algorithm of Schaeffer et al. (27), which is a special algorithm for the case of zero error covariances, was used to analyze data on survival scores of 1 to 5. This algorithm is a form of Fisher's scoring method. Therefore, to ensure that pa-

TABLE 1. Summary statistics for Holstein-Friesian (HF) and Jersey (J) analyses.[1]

| | Analysis | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1[2] | | 2a | | 2b | | 3 | | 4 | |
| | HF | J | HF | J | HF | J | HF | J | HF | J |
| Records, no. | 190,830 | 41,964 | 143,250 | 32,003 | 19,269 | 8768 | 14,596 | 4695 | 10,888 | 3269 |
| Sires, no. | 423 | 382 | 1242 | 300 | 442 | 170 | 334 | 125 | 389 | 107 |
| Percentage of data by fixed sires | 0 | 0 | 18 | 48 | 46 | 71 | 0 | 0 | 0 | 0 |
| Mean NZ,[3] % | 12 | 30 | 1 | 49 | 1 | 30 | 6 | 45 | 5 | 41 |
| Mean NA,[4] % | 38 | 8 | 32 | 2 | 8 | 0 | 26 | 3 | 25 | 4 |

[1] Analysis 1 = survival, 2 = production and stayability for opportunity group until lactation 2 (2a) or until lactation 6 (2b), 3 = production and workability, 4 = production and type.

[2] Pertaining to survival during lactation 1.

[3] NZ = Percentage of New Zealand genes of sires.

[4] NA = Percentage of North American genes of sires.

rameter estimates were within the parameter space, negative eigenvalues of the between-sire covariance matrix were arbitrarily set to 1% of the mean eigenvalue at each round of iteration (11). Mean eigenvalues were always positive.

Computer hardware limitations restricted the number of traits × number of sires to approximately 2500. Therefore, ≤500 sires with the largest number of first lactation progeny were selected. Thus, the bulls represented in the data were a sample of the older bulls. (Selection of bulls on the number of progeny was only for analyses of survival scores and was not carried out for subsequent analyses.) Furthermore, to achieve sufficient accuracy of parameter estimates, all bulls were considered to be random effects. Therefore, a downward bias in heritability estimates was expected if selection had occurred on survival or traits correlated with survival. The tradeoff between bias and accuracy was considered to be justified in this case. For the J data, no restriction was applied because of the relatively small amount of data.

The model fitted to each survival score was

$$\begin{aligned} S_i = {} & \text{HYS} + \text{MC} + \text{BC} + \text{group} + \text{sire} \\ & + (b_i \times \text{NZ}) + (b_2 \times \text{NA}) \\ & + (b_3 \times \text{age}) + \text{residual} \end{aligned}$$

with

$S_i$ = survival score for lactation i (0 or 100),
HYS = herd-year-season of calving (four seasons per herd-year: December to March, April to June, July to August, and September to November),
MC = month of calving (1 to 12),
BC = breed code of the dam (five levels; unknown, HF, J, HF × J, and J × HF),
group = sire group based on year of birth (seven groups: ≤1970, 1971 to 1975, 1976 to 1977, 1978 to 1979, 1980 to 1981, 1982 to 1983, and 1984 to 1986),
$b_i$ = regression coefficient,
NZ = percentage of New Zealand genes of the sire,
NA = percentage of North American genes of the sire, and
age = age at first calving (months).

The percentage of New Zealand and North American genes of each bull were estimated from the country of origin code (1) of the bull, its sire, and its maternal grandsire. A detailed description of the data for the survival analysis is given in Table 2.

*Analyses of Yield Traits and Stayability.* First lactation records for milk, fat, and protein yields and their corresponding test day deviations, lactation length, and stayability records were analyzed simultaneously using the algorithm described by Meyer (16). One model was assumed to be appropriate for all traits; the analyses were performed with equal design matrices.

*Age at First Calving.* A preliminary analysis was carried out in which age at first calving was fitted as a dependent variable. From this analysis, relatively high heritabilities were estimated for age at first calving (.20 and .15 for HF and J). These heritability estimates suggested that some confounding may have existed for sires and the time of year that their progeny were born (and for the time that they were mated and subsequently calved). When day of birth (from 1 to 365) of progeny of sires was fitted as a dependent variable, significant

TABLE 2. Description of data for survival analyses for Holstein-Friesian (HF) and Jersey (J) cattle.

| | Survival score | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| | HF | J | HF | J | HF | J | HF | J | HF | J |
| Mean, % | 83 | 83 | 83 | 80 | 84 | 81 | 82 | 79 | 80 | 77 |
| Records, no. | 190,830 | 41,964 | 164,911 | 43,824 | 104,702 | 28,704 | 63,940 | 18,159 | 37,247 | 10,798 |
| Sires, no. | 423 | 382 | 405 | 345 | 387 | 317 | 329 | 275 | 272 | 224 |

heritabilities were estimated (.70 and .28 for HF and J). The use of a young bull over a short time was confirmed by analysts from the AI industry (S. McClintock, 1993, personal communication). To overcome potential biases in parameter estimates, age at first calving was fitted in the model along with a herd-year-season of birth, month of birth (from 1 to 12), and month of calving (from 1 to 12). A herd-year-season of birth was also fitted by Moore et al. (21), who argued for treating age at calving as a covariable rather than as a dependent variable.

Yield and stayability records were analyzed using

$$
\begin{aligned}
y = {} & \text{HYSB} + \text{MB} + \text{MC} + \text{BC} + \text{country} \\
& + \text{group} + \text{sire} + (b_1 \times \text{NZ}) + (b_2 \times \text{NA}) \\
& + (b_3 \times \text{age}) + \text{residual}
\end{aligned}
$$

with

y = record of stayability and first lactation yield,
HYSB = herd-year-season of birth (four seasons per year),
MB = month of birth (1 to 12),
country = country of origin of sire (Australia or rest of the world), and
sire = fixed or random sire.

Sires were considered to be fixed if the number of years from the birth of the sire to the first calving of his progeny was ≥8 yr. Fixed sires were included in the analysis to improve the data structure (17, 30). Only records of those fixed sires with >5000 and 1000 progeny (for HF and J, respectively) were included.

For both breeds, separate data files were extracted: one for cows that had the opportunity to start a second lactation (opportunity group $\text{STAY}_2$) and another for cows that had the opportunity to stay until lactation 6 (opportunity group $\text{STAY}_6$). For the first data file, the primary interest was in the parameters for first lactation yield and their correlation with early survival (survival from lactation 1 to 2). The second data file was analyzed to obtain correlations between several stayabilities and their correlation with first lactation milk records. The latter data were necessarily from a smaller number of dams and sires, so parameter estimates were expected to be less precise. A full description of the data is in Table 3.

*Analysis of Workability and Yield.* After data on workability and milk yield were matched, relatively few records were obtained (Table 1). To estimate genetic parameters with reasonable standard errors, all sires were treated as random effects. Treatment of all sires as random effects may bias parameters

TABLE 3. Mean and standard deviation of analyses[1] of stayability and yield for Holstein-Friesian (HF) and Jersey (J) cattle.

| | Analysis | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 2a | | | | 2b | | | |
| Trait | HF | J | HF | J | HF | J | HF | J |
| | $\bar{X}$ | $\bar{X}$ | SD | SD | $\bar{X}$ | $\bar{X}$ | SD | SD |
| Lactation length, d | 294 | 282 | 63 | 60 | 291 | 282 | 59 | 61 |
| Milk yield, L | 3907 | 2837 | 1163 | 800 | 3608 | 2769 | 1027 | 788 |
| Fat yield, kg | 162 | 149 | 48 | 44 | 153 | 144 | 45 | 42 |
| Protein yield, kg | 124 | 102 | 37 | 30 | 116 | 101 | 33 | 29 |
| Milk deviation, L | 45 | −191 | 640 | 551 | 49 | −184 | 622 | 554 |
| Fat deviation, kg | −1 | −3 | 24 | 24 | 0 | −2 | 25 | 24 |
| Protein deviation, kg | 3 | −1 | 18 | 17 | 3 | 0 | 18 | 18 |
| $\text{STAY}_2$,[2] % | 82 | 83 | 38 | 38 | 84 | 84 | 36 | 37 |
| $\text{STAY}_3$, % | | | | | 71 | 69 | 45 | 46 |
| $\text{STAY}_4$, % | | | | | 61 | 57 | 49 | 49 |
| $\text{STAY}_5$, % | | | | | 52 | 46 | 50 | 50 |
| $\text{STAY}_6$, % | | | | | 43 | 36 | 50 | 48 |

[1] Analysis 2a, for cows with opportunity until lactation 2; 2b, for cows with opportunity until lactation 6.

[2] $\text{STAY}_i$ = Stayability until the start of lactation i.

for stayabilities and yield, but less so for the workability traits, because these have been recorded only since 1987, and less selection has been practiced on them.

A multivariate analysis was performed using Model [2] with only two seasons (January to June and July to December) per herd-year of birth. Table 4 shows some characteristics of these data.

*Analysis of Type and Yield.* Fewer records on type traits were available than on workability traits (Table 1). Therefore, all sires were treated as random effects for the joint analyses of type and yield data. When the algorithm of Meyer (16) was used, only one main effect for contemporary group, which is the same for all traits, could be fitted. Different effects for contemporary group could apply to yield and type data, particularly because date of classification and classifier were available for the type data. However, cows that belong to the same herd-year-season of birth were also likely to be classified on the same round of classification, and usually only one classifier scored the cows on a particular round. Therefore, the same model (Model [2]) was assumed to be appropriate for yield and type traits. A separate analysis of the type traits only, when a herd-round-classifier effect was fitted as the main effect for contemporary group, resulted in very similar parameter estimates for the type traits as the estimates shown herein. Results from this analysis on type traits alone are not shown. Only two sire groups were fitted: bulls born before and after 1981. A summary of the joint type and yield data is in Table 5.

## RESULTS AND DISCUSSION

### Survival Analyses

Estimates of genetic parameters for survival scores of 1 to 5 are in Table 6. For HF and J, heritabilities were generally low. The average heritabilities over all five survival scores were .03 and .05 for HF and J, respectively. Genetic correlations between survival during different lactations were very high, in particular the correlations between adjacent survival scores. The average correlation between survivals was .76 and .97 for HF and J; the average correlation between adjacent survivals was .91 and .98 for HF and J. These results suggest that survival for different lactations could be treated as the same trait. This result is somewhat surprising because culling during the first few lactations was expected to be associated with a different set of traits than culling later in life. Although the mean and standard deviation of survival scores of 6 to 10 were different (results not shown), the economic weights for those later survivals is small (32), so that a repeatability model with homogeneous variances applied to survival scores of 1 to 5 seems to be justified. At present, ADHIS calculates ABV for survival using a repeatability model with a heritability of .025 (L. Jones, 1993, personal communication).

As expected from the method of data extraction (selection on the number of first lactation records per sire), the standard errors on correlations between early and later survivals

TABLE 4. Mean and standard deviation for combined data of workability and first lactation yield for Holstein-Friesian (HF) and Jersey (J) cattle.

| Trait | HF | | J | |
|---|---|---|---|---|
| | $\overline{X}$ | SD | $\overline{X}$ | SD |
| Age, mo | 24.5 | 1.7 | 24.4 | 1.2 |
| Milk yield, L | 3979 | 998 | 2932 | 747 |
| Fat yield, kg | 168 | 42 | 155 | 41 |
| Protein yield, kg | 125 | 32 | 105 | 27 |
| Milking speed, 1 to 5 | 2.7 | .8 | 2.6 | .8 |
| Temperament, 1 to 5 | 2.6 | .9 | 2.5 | .8 |
| Likeability, 1 to 5 | 2.6 | .9 | 2.7 | .9 |
| $STAY_2$,[1] % | 85 | 36 | 82 | 38 |
| $STAY_3$, % | 72 | 45 | 66 | 47 |
| $STAY_4$, % | 60 | 49 | 53 | 50 |

[1] $STAY_i$ = Stayability until the start of lactation i.

TABLE 5. Mean and standard deviation for combined data of type and first lactation yield for Holstein-Friesian (HF) and Jersey (J) cattle.

| Trait | HF | | J | |
|---|---|---|---|---|
| | $\bar{X}$ | SD | $\bar{X}$ | SD |
| Age at calving, mo | 25.1 | 2.4 | 24.4 | 1.3 |
| Milk yield, L | 3845 | 994 | 2927 | 749 |
| Fat yield, kg | 160 | 43 | 154 | 41 |
| Protein yield, kg | 122 | 32 | 105 | 28 |
| Overall type, 1 to 18 | 7.8 | 1.7 | 8.4 | 1.7 |
| Dairy character, 1 to 18 | 10.3 | 1.8 | 10.5 | 1.8 |
| Capacity, 1 to 18 | 10.0 | 2.0 | 10.4 | 1.9 |
| Feet and legs, 1 to 18 | 8.7 | 1.6 | 9.0 | 1.5 |
| Mammary system, 1 to 18 | 8.3 | 1.7 | 9.0 | 1.7 |
| Size, 1 to 9 | 4.8 | 1.3 | 5.1 | 1.2 |
| Height, 1 to 9 | 4.2 | 1.5 | 4.5 | 1.3 |
| Angularity, 1 to 9 | 5.3 | 1.2 | 5.4 | 1.2 |
| Rear set legs, 1 to 9 | 5.8 | 1.1 | 5.9 | .9 |
| Fore udder attachment, 1 to 9 | 4.4 | 1.0 | 4.8 | 1.1 |
| Rear attachment height, 1 to 9 | 4.6 | 1.1 | 5.1 | 1.0 |
| Medial suspensory ligament, 1 to 9 | 5.5 | 1.1 | 5.6 | 1.1 |
| Fore teat placement, 1 to 9 | 4.5 | 1.2 | 4.8 | 1.2 |
| STAY$_2$,[1] % | 85 | 35 | 82 | 38 |
| STAY$_3$, % | 73 | 45 | 66 | 47 |
| STAY$_4$, % | 62 | 49 | 53 | 50 |

[1] STAY$_i$ = Stayability until the start of lactation i.

were large, in particular for J. For example, standard errors for correlations between survival scores for lactation 5 and other lactations were approximately .30.

### Analyses of Yield and Stayability

An estimate of the correlation matrix of first lactation traits is in Table 7. Heritabilities and correlations were consistently higher for J data. The mean heritability for milk, fat, and protein yield was .22 and .27 for HF and J; the means for test day deviations were .30 and .37 for HF and J, respectively. Hence, heritabilities for test day deviations were approximately 40% higher than the corresponding heritabilities for lactation yields. Meyer et al. (20) estimated

TABLE 6. Estimates (Est.) of genetic parameters[1] for survival analyses for Holstein-Friesian (HF) and Jersey (J) cattle.[2]

| | | Survival score[3] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Breed | $S_1$ | | $S_2$ | | $S_3$ | | $S_4$ | | $S_5$ | |
| | | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE |
| $S_1$ | HF | .03 | .00[4] | | | | | | | | |
| | J | .07 | .01 | | | | | | | | |
| $S_2$ | HF | .95 | .03 | .03 | .00 | | | | | | |
| | J | .96 | .04 | .08 | .02 | | | | | | |
| $S_3$ | HF | .76 | .08 | .81 | .07 | .02 | .00 | | | | |
| | J | .95 | .07 | .99 | .05 | .04 | .01 | | | | |
| $S_4$ | HF | .67 | .10 | .79 | .09 | .96 | .06 | .02 | .01 | | |
| | J | .94 | .15 | .97 | .14 | .98 | .16 | .02 | .01 | | |
| $S_5$ | HF | .37 | .15 | .57 | .13 | .80 | .11 | .92 | .08 | .03 | .01 |
| | J | .96 | .26 | .98 | .25 | .98 | .27 | .97 | .36 | .02 | .01 |

[1] Heritabilities are on diagonal; genetic correlations below diagonal.

[2] Phenotypic standard deviations of survival scores ranged from 35 to 40%.

[3] $S_i$ = Probability of survival during lactation i.

[4] Standard error of .00 means <.005.

TABLE 7. Estimates (Est.) of genetic parameters[1] and their standard errors[2] for stayability until lactation 2 ($STAY_2$) and first lactation yield for Holstein-Friesian (HF) and Jersey (J) cattle.

| Trait[3] | Breed | LL | | $STAY_2$ | | M | | F | | P | | MDEV | | FDEV | | PDEV | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE |
| LL | HF | .08 | .01 | .43 | | .80 | | .81 | | .83 | | .37 | | .33 | | .39 | |
| | J | .14 | .01 | .50 | | .79 | | .82 | | .83 | | .41 | | .41 | | .44 | |
| $STAY_2$ | HF | .71 | .05 | .05 | .01 | .32 | | .34 | | .33 | | .23 | | .24 | | .25 | |
| | J | .79 | .09 | .07 | .02 | .39 | | .41 | | .40 | | .29 | | .29 | | .29 | |
| M | HF | .79 | .03 | .62 | .05 | .24 | .02 | .91 | | .97 | | .79 | | .63 | | .76 | |
| | J | .87 | .04 | .90 | .07 | .28 | .04 | .93 | | .97 | | .83 | | .72 | | .79 | |
| F | HF | .79 | .03 | .64 | .05 | .78 | .02 | .20 | .01 | .94 | | .64 | | .75 | | .70 | |
| | J | .89 | .03 | .86 | .07 | .89 | .02 | .26 | .04 | .96 | | .70 | | .79 | | .74 | |
| P | HF | .84 | .02 | .69 | .05 | .93 | .01 | .86 | .01 | .21 | .02 | .71 | | .64 | | .76 | |
| | J | .91 | .03 | .86 | .07 | .96 | .01 | .95 | .01 | .26 | .04 | .75 | | .72 | | .79 | |
| MDEV | HF | .54 | .05 | .47 | .06 | .93 | .01 | .64 | .03 | .81 | .02 | .33 | .02 | .77 | | .92 | |
| | J | .79 | .06 | .90 | .07 | .99 | .01 | .84 | .04 | .91 | .02 | .39 | .05 | .84 | | .92 | |
| FDEV | HF | .49 | .05 | .47 | .06 | .63 | .03 | .91 | .01 | .70 | .03 | .63 | .03 | .29 | .02 | .84 | |
| | J | .81 | .06 | .85 | .08 | .86 | .03 | .98 | .01 | .91 | .02 | .83 | .03 | .37 | .05 | .90 | |
| PDEV | HF | .53 | .05 | .53 | .06 | .83 | .02 | .73 | .03 | .89 | .01 | .88 | .01 | .74 | .02 | .29 | .02 |
| | J | .85 | .05 | .85 | .08 | .96 | .01 | .93 | .02 | .99 | .01 | .93 | .01 | .91 | .02 | .35 | .05 |

[1] Heritabilities are on diagonal, genetic correlations below diagonal, and phenotypic correlations above diagonal.

[2] All standard errors for phenotypic correlations were ≤.01.

[3] LL = Lactation length, M = milk yield, F = fat yield, P = protein yield, MDEV = test day deviation for milk, FDEV = test day deviation for fat, and PDEV = test day deviation for protein.

TABLE 8. Estimates (Est.) of genetic parameters[1] and their standard errors[2] for stayabilities and their correlation with first lactation yield for Holstein-Friesian (HF) and Jersey (J) cattle.

| Trait[3] | Breed | $STAY_2$ | | $STAY_3$ | | $STAY_4$ | | $STAY_5$ | | $STAY_6$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE |
| $STAY_2$ | HF | .05 | .01 | .66 | | .52 | | .43 | | .35 | |
| | J | .22 | .06 | .65 | | .50 | | .40 | | .32 | |
| $STAY_3$ | HF | .86 | .06 | .07 | .02 | .79 | | .65 | | .53 | |
| | J | .72 | .11 | .21 | .06 | .76 | | .61 | | .48 | |
| $STAY_4$ | HF | .86 | .08 | .98 | .02 | .07 | .02 | .82 | | .67 | |
| | J | .68 | .14 | .99 | .01 | .13 | .05 | .79 | | .63 | |
| $STAY_5$ | HF | .83 | .11 | .98 | .03 | .99 | .01 | .07 | .02 | .82 | |
| | J | .79 | .14 | .86 | .08 | .88 | .07 | .14 | .05 | .79 | |
| $STAY_6$ | HF | .66 | .16 | .91 | .06 | .92 | .04 | .92 | .03 | .03 | .01 |
| | J | .80 | .15 | .92 | .06 | .93 | .04 | .97 | .03 | .06 | .03 |
| Y | HF | .49 | .14 | .72 | .08 | .65 | .10 | .68 | .10 | .81 | .08 |
| | J | .75 | .11 | .91 | .07 | .87 | .13 | .72 | .17 | .78 | .20 |
| YDEV | HF | .60 | .12 | .72 | .08 | .69 | .09 | .70 | .10 | .80 | .07 |
| | J | .70 | .12 | .91 | .07 | .87 | .12 | .73 | .16 | .77 | .18 |

[1] Heritabilities are on diagonals, genetic correlations below, and phenotypic correlations above diagonals.

[2] All standard errors for phenotypic correlations were ≤.01.

[3] $STAY_i$ = Stayability until lactation i; Y = standardized average of milk, fat, and protein yield; and YDEV = standardized average of test day deviation for milk, fat, and protein.

heritabilities for individual test day yields from HF data and created linear combinations of those traits (canonical variables). Heritabilities for canonical variables based on ≥6 test days were approximately .37, .26, and .29 for milk, fat, and protein and should be considered to be upper limits for the heritabilities of the test day deviations. They were very similar to the heritabilities for milk, fat, and protein deviations from Table 7. Hence, for pasture-based production systems, accounting for the environmental variation on test days removes a substantial amount of error variance and can be recommended for prediction of breeding values in other countries.

The test day deviations are less influenced by lactation length than are conventional 305-d yields because only test days on which a cow is present are included in her average test day deviation and are reflected in higher phenotypic correlations of lactation length with lactation yields than with deviations and higher corresponding genetic correlations for the HF data. This result explains why lactation yields and deviations are not genetically identical traits for HF; genetic correlations were approximately .90 (Table 7).

The heritability for survival until lactation 2 (survival during lactation 1 = $STAY_2$) was .05 compared with .03 from Table 6. The heritability for $STAY_2$ of .05 (Table 7) is unlikely to be biased by selection and is larger than the estimate of .03 from the survival analyses. Perhaps a reasonable assumption for the average heritability of survival during lactations 1 to 5 is .05. However, heritabilities for survival could be biased upward if progeny of sires survive longer because of traits associated with the sire that do not reflect the real ability of daughters to survive (e.g., semen price).

The heritabilities for lactation length were .08 for HF and .14 for J data. The genetic correlation of lactation length and yield traits was high, approximately .80 and .90 with first lactation records for HF and J.

Table 8 shows the correlation matrix for $STAY_2$ to $STAY_6$ and the genetic correlations of stayabilities with first lactation yields. Heritabilities for different stayabilities were similar, and heritabilities were consistently higher for J. Because stayability is a combination of survival scores up to a certain age, the genetic parameters for stayabilities and survivals should correspond. The means of $STAY_3$ to $STAY_6$ were closer to 50% than those of survival scores, so heritabilities were expected to be greater. Also, the genetic correlations between stayabilities should be higher than among survival scores because of their part-whole relationship. These expectations were realized (Tables 6 and 8).

Stayability was highly correlated with yield traits, on average .65 and .87 for complete lactation yields and .49 and .87 for test day deviations for HF and J, respectively. Correlations between first lactation yield traits and $\mathrm{STAY}_6$ were approximately .80 for HF and J data. Heritabilities for first lactation yield traits were lower than the corresponding estimates from Table 7, suggesting that the bulls represented in opportunity group $\mathrm{STAY}_6$ were a selected group.

Why genetic parameters should be consistently different for HF and J data was not obvious. The higher phenotypic correlations between yield traits and $\mathrm{STAY}_2$ (Table 7) imply that J cows were culled more heavily on yield than were HF cows. Mean survival scores for lactation 1 were similar for HF and J cows (Table 3), but for later lactations were slightly lower for J. Perhaps J farmers, in general, cull more heavily on yield than their colleagues with HF cows. For the analyses of survival scores, bias in the HF estimates may have been greater because of selection of bulls, but this was not the case for other analyses.

Heritability of herd life (the sum of stayabilities for all age groups) was expected to be higher than that for individual survival traits if genetic correlations between survivals were high and if heritabilities for survival scores were similar. Visscher et al. (32) showed that the heritability of herd life is expected to be approximately three to five times that of survival.

### Analyses of Yield and Workability

Estimates of the covariance matrix for milking speed, temperament, and likeability and their genetic correlations with first lactation yield traits and with stayability scores are in Table 9. Heritabilities for all three workability traits were similar (.18 to .26 for HF and .25 to

TABLE 9. Estimates (Est.) of genetic parameters[1] and their standard errors[2] for workability traits and their correlation with first lactation yield and stayabilities for Holstein-Friesian (HF) and Jersey (J) cattle.[3]

| | | Trait | | | | | |
|---|---|---|---|---|---|---|---|
| Trait[4] | Breed | MS | | TEMP | | LIKE | |
| | | Est. | SE | Est. | SE | Est. | SE |
| MS | HF | .26 | .04 | .18 | | .31 | |
| | J | .29 | .07 | .19 | | .31 | |
| TEMP | HF | .53 | .09 | .22 | .03 | .56 | |
| | J | .57 | .14 | .25 | .06 | .54 | |
| LIKE | HF | .58 | .08 | .79 | .05 | .18 | .03 |
| | J | .69 | .12 | .61 | .12 | .26 | .06 |
| M | HF | .06 | .11 | –.11 | .12 | –.50 | .09 |
| | J | –.34 | .17 | –.17 | .18 | –.80 | .08 |
| F | HF | –.05 | .12 | –.18 | .12 | –.52 | .09 |
| | J | –.28 | .18 | .00 | .19 | –.64 | .11 |
| P | HF | .05 | .11 | –.13 | .11 | –.47 | .09 |
| | J | –.30 | .17 | –.17 | .18 | –.82 | .07 |
| $\mathrm{STAY}_2$ | HF | –.38 | .14 | –.26 | .15 | –.55 | .13 |
| | J | –.64 | .15 | –.72 | .11 | –.92 | .05 |
| $\mathrm{STAY}_3$ | HF | –.14 | .16 | –.22 | .16 | –.52 | .13 |
| | J | –.56 | .14 | –.38 | .16 | –.93 | .03 |
| $\mathrm{STAY}_4$ | HF | –.23 | .16 | –.19 | .17 | –.54 | .14 |
| | J | –.52 | .15 | –.30 | .18 | –.91 | .04 |

[1] Heritabilities are on diagonals, genetic correlations below, and phenotypic correlations above diagonals.

[2] All standard errors for phenotypic correlations were ≤.02.

[3] Phenotypic standard deviations for MS, TEMP, and LIKE ranged from .7 to .8.

[4] MS = Milking speed, TEMP = temperament, LIKE = likeability, M = milk yield, F = fat yield, P = protein yield, and $\mathrm{STAY}_i$ = stayability until lactation i.

.29 for J) and were slightly higher for J data. Previous heritability estimates of milking speed, although often imprecise, have been .15 to .46 for objective measures (9, 23, 33) and .14 to .32 for subjective scores (8, 18). Assuming that the genetic correlation is high between subjective evaluation by farmers of milking speed and a direct measure of milking speed [(see references in (18)], the results suggest that direct measurements of milking speed using a stopwatch are not necessary (and too expensive). Erf et al. (9) estimated the heritability of overall satisfaction (identical in definition to likeability) to be .18.

Genetic correlations between workability traits were surprisingly high but perhaps reflect how some farmers score for these traits, i.e., by giving similar scores for all workability traits to a particular cow. However, the correlation between temperament and milking speed may also reflect a cause and effect relationship; i.e., cows with bad temperament take longer to milk because they kick off the cups more frequently or let down milk relatively slowly. Erf et al. (9) reported a genetic correlation of .36 between milking speed and overall satisfaction, although the standard error of the estimate was large. Genetic correlations between milking speed, temperament, and yield traits for first lactation were not significantly different from zero for HF data. Higher yielding J cows tended to have a lower score for milking speed (indicating faster milkers). Genetic correlations of likeability with yield traits were approximately –.50 and –.75 for HF and J, respectively, which means that higher yielding cows were more likeable. The genetic correlation between milking speed and milk yield, which was approximately zero, implies that farmers adjusted for the milk yield of the cow when they assessed her milking speed. Meyer and Burnside (18) found a similar result.

Unfortunately, standard errors for genetic correlations between workability traits and stayabilities were large (Table 9). Heritabilities for stayabilities were substantially lower than heritabilities estimated from the larger data file for yield (see Tables 3 and 8). For HF data, genetic correlations between milking speed, temperament, and stayabilities were approximately –.20 to –.30 and were more negative for $STAY_2$ than for later stayabilities. For J data, the correlations were approximately twice as large as those for HF. For our selection index program, we corrected the survival ABV for yield and workability traits, assuming a genetic correlation of –.20 between survival and milking speed and survival and temperament (Bowman, Visscher, and Goddard, 1994, unpublished).

Stayabilities and likeability were most highly correlated: a correlation of –.91 between likeability and $STAY_4$ for J was very large (Table 9). Likeability is a composite trait and was expected to be correlated with other traits. A genetic regression of likeability on milking speed, temperament, and milk yield, using the correlations for HF from Table 9, resulted in an accuracy of 90% for prediction of likeability. A separate joint analysis of workability and type traits (results not shown) estimated a genetic correlation of –.50 and –.70 between likeability and overall type for HF and J, respectively. Therefore, a linear combination of yield traits, milking speed, temperament, and overall type probably is adequate for predicting likeability; likeability does not provide extra information if the other traits are available. Alternatively, a trait such as likeability is inexpensive to measure, and, if the trait is of interest for selection purposes, scoring of traits that are much more expensive to measure (e.g., type traits) could be omitted.

### Analyses of Yield and Type

The covariance matrix for 13 type traits and their phenotypic and genetic correlations with milk yield and stayability scores are in Tables 10 and 11. Despite the relatively large standard errors of the estimates of genetic correlations, parameters for HF and J were similar. Heritabilities for type traits ranged from .11 to .35 for HF and from .15 to .48 for J; for both breeds, the lowest heritabilities were for feet and legs, and the highest were for dairy character. Overall type was highly correlated with all other traits for HF and J. Overall type and mammary system were essentially the same trait genetically; genetic correlations were .97 and .96 for HF and J, respectively. Height and size were highly correlated, .81 and .84 for HF and J, respectively. As expected, the summary trait of mammary system was highly correlated with all linear udder traits.

Phenotypic correlations between type traits and first lactation yield were low and similar

TABLE 10. Estimates (Est.) of genetic parameters[1] and their standard errors[2] for type traits for Holstein-Friesian (HF) and Jersey (J) cattle.[3]

| Trait[4] | Breed | OT | | DC | | CAP | | F&L | | MAM | | SIZE | | HGHT | | ANG | | RLS | | FUA | | RAH | | MSL | | FTP | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE |
| OT | HF | .26 | .04 | .57 | | .39 | | .44 | | .87 | | .30 | | .26 | | .18 | | –.08 | | .53 | | .55 | | .53 | | .44 | |
| | J | .37 | .09 | .56 | | .32 | | .41 | | .85 | | .26 | | .19 | | .16 | | –.17 | | .54 | | .53 | | .58 | | .47 | |
| DC | HF | .74 | .05 | .35 | .04 | .33 | | .30 | | .46 | | .24 | | .22 | | .48 | | .03 | | .22 | | .39 | | .33 | | .21 | |
| | J | .83 | .06 | .48 | .10 | .22 | | .23 | | .43 | | .17 | | .14 | | .51 | | –.08 | | .19 | | .35 | | .34 | | .22 | |
| CAP | HF | .60 | .07 | .51 | .08 | .34 | .04 | .29 | | .24 | | .75 | | .53 | | –.17 | | –.09 | | .16 | | .15 | | .14 | | .09 | |
| | J | .49 | .16 | .32 | .19 | .17 | .06 | .32 | | .18 | | .76 | | .53 | | –.25 | | –.14 | | .17 | | .11 | | .08 | | .05 | |
| F&L | HF | .61 | .08 | .40 | .10 | .70 | .07 | .11 | .02 | .32 | | .23 | | .16 | | .04 | | –.27 | | .21 | | .23 | | .20 | | .15 | |
| | J | .56 | .14 | .45 | .16 | .30 | .21 | .15 | .04 | .28 | | .27 | | .20 | | –.06 | | –.46 | | .21 | | .20 | | .22 | | .14 | |
| MAM | HF | .97 | .01 | .66 | .06 | .44 | .08 | .43 | .10 | .28 | .04 | .18 | | .16 | | .18 | | –.05 | | .61 | | .61 | | .59 | | .52 | |
| | J | .96 | .02 | .77 | .09 | .38 | .19 | .53 | .15 | .33 | .08 | .15 | | .10 | | .16 | | –.12 | | .62 | | .60 | | .66 | | .56 | |
| SIZE | HF | .50 | .08 | .47 | .08 | .94 | .01 | .65 | .09 | .34 | .09 | .28 | .04 | .69 | | –.16 | | –.08 | | .13 | | .12 | | .11 | | .08 | |
| | J | .39 | .17 | .36 | .17 | .75 | .09 | .17 | .21 | .30 | .18 | .17 | .05 | .68 | | –.23 | | –.13 | | .15 | | .08 | | .06 | | .07 | |
| HGHT | HF | .41 | .09 | .43 | .08 | .63 | .06 | .49 | .10 | .31 | .10 | .81 | .04 | .32 | .04 | .00 | | –.06 | | .11 | | .12 | | .10 | | .07 | |
| | J | .08 | .18 | .10 | .18 | .53 | .15 | –.10 | .20 | .02 | .19 | .89 | .04 | .42 | .10 | –.11 | | –.09 | | .09 | | .05 | | .04 | | .05 | |
| ANG | HF | .47 | .09 | .77 | .05 | .01 | .11 | .13 | .12 | .46 | .09 | .03 | .11 | .29 | .10 | .22 | .03 | –.10 | | .07 | | .19 | | .15 | | .10 | |
| | J | .54 | .14 | .81 | .07 | –.03 | .21 | .26 | .19 | .48 | .15 | .34 | .18 | .18 | .18 | .32 | .07 | .09 | | .01 | | .17 | | .17 | | .10 | |
| RLS | HF | –.23 | .11 | –.04 | .11 | –.36 | .10 | –.68 | .08 | –.13 | .11 | –.38 | .10 | –.27 | .11 | .15 | .12 | .19 | .03 | –.05 | | –.05 | | –.01 | | –.03 | |
| | J | –.52 | .15 | –.47 | .16 | –.07 | .22 | –.74 | .10 | –.47 | .16 | –.06 | .20 | .07 | .19 | –.46 | .17 | .19 | .05 | –.09 | | –.10 | | –.11 | | –.07 | |
| FUA | HF | .81 | .05 | .34 | .10 | .38 | .11 | .44 | .12 | .86 | .03 | .31 | .11 | .32 | .11 | .15 | .12 | –.25 | .12 | .15 | .03 | .32 | | .36 | | .36 | |
| | J | .55 | .15 | .37 | .18 | .35 | .22 | .45 | .19 | .60 | .14 | .28 | .21 | .09 | .21 | .28 | .20 | –.33 | .20 | .21 | .07 | .33 | | .36 | | .36 | |
| RAH | HF | .77 | .04 | .67 | .06 | .31 | .09 | .21 | .12 | .81 | .04 | .29 | .10 | .33 | .09 | .47 | .09 | –.10 | .11 | .62 | .08 | .29 | .04 | .42 | | .22 | |
| | J | .63 | .11 | .75 | .08 | .36 | .19 | .58 | .14 | .64 | .12 | .05 | .19 | –.16 | .18 | .34 | .16 | –.47 | .15 | .45 | .17 | .23 | .06 | .42 | | .23 | |
| MSL | HF | .73 | .06 | .49 | .08 | .32 | .10 | .21 | .13 | .80 | .05 | .20 | .11 | .22 | .11 | .39 | .10 | –.01 | .12 | .55 | .09 | .63 | .07 | .19 | .03 | .48 | |
| | J | .87 | .05 | .67 | .10 | .29 | .20 | .77 | .09 | .83 | .06 | .31 | .18 | .03 | .18 | .55 | .13 | –.70 | .11 | .54 | .15 | .45 | .15 | .36 | .08 | .57 | |
| FTP | HF | .67 | .06 | .25 | .09 | .26 | .09 | .37 | .11 | .71 | .05 | .18 | .10 | .17 | .10 | .20 | .10 | –.15 | .11 | .57 | .08 | .28 | .09 | .73 | .06 | .31 | .04 |
| | J | .78 | .08 | .61 | .12 | .05 | .21 | .51 | .16 | .74 | .09 | .20 | .19 | .04 | .18 | .63 | .12 | –.73 | .10 | .40 | .18 | .27 | .17 | .90 | .04 | .31 | .07 |

[1] Heritabilities on diagonals, genetic correlations below, and phenotypic correlations above diagonals.

[2] All standard errors for phenotypic correlations were ≤.03.

[3] Phenotypic standard deviations ranged from .8 to 1.1 for traits on a 9-point scale and 1.3 to 1.7 for traits on an 18-point scale.

[4] OT = Overall type, DC = dairy character, CAP = capacity, F&L = feet and legs, MAM = mammary system, HGHT = height, ANG = angularity, RLS = rear legs set, FUA = fore udder attachment, RAH = rear attachment height, MSL = medial suspensory ligament, and FTP = fore teat placement.

TABLE 11. Estimates (Est.) of genetic parameters[1] and their standard errors[2] between type traits and first lactation milk yield and stayabilities for Holstein-Friesian (HF) and Jersey (J) cattle..

| Correlation | Trait[4] | Breed | Trait[3] OT |  | DC |  | CAP |  | F&L |  | MAM |  | SIZE |  | HGHT |  | ANG |  | RLS |  | FUA |  | RAH |  | MSL |  | FTP |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE | Est. | SE |
| RG | M | HF | .31 | .10 | .50 | .08 | .24 | .10 | .22 | .12 | .25 | .10 | .20 | .10 | .09 | .11 | .22 | .11 | .05 | .12 | .08 | .12 | .26 | .10 | .10 | .11 | –.04 | .11 |
|  |  | J | .62 | .12 | .84 | .06 | .10 | .20 | .09 | .19 | .60 | .13 | .17 | .18 | –.08 | .17 | .76 | .08 | –.28 | .17 | .18 | .20 | .51 | .13 | .37 | .15 | .40 | .15 |
|  | STAY$_2$ | HF | .09 | .13 | .35 | .12 | .24 | .12 | .14 | .15 | .04 | .13 | .20 | .13 | .11 | .13 | .14 | .13 | .17 | .14 | –.06 | .15 | –.24 | .12 | .04 | .14 | .11 | .13 |
|  |  | J | .26 | .19 | .47 | .16 | –.18 | .22 | –.31 | .19 | .25 | .19 | .17 | .20 | .06 | .19 | .73 | .11 | –.01 | .21 | .05 | .22 | –.08 | .19 | .12 | .19 | .31 | .18 |
|  | STAY$_3$ | HF | .13 | .13 | .28 | .12 | .19 | .13 | .11 | .13 | .11 | .13 | .20 | .13 | .13 | .13 | .02 | .14 | .17 | .14 | .09 | .15 | –.09 | .13 | .03 | .14 | .10 | .13 |
|  |  | J | .54 | .15 | .70 | .11 | .06 | .22 | .06 | .20 | .48 | .16 | .31 | .18 | .09 | .19 | .82 | .09 | –.35 | .18 | .22 | .21 | .21 | .18 | .41 | .16 | .52 | .15 |
|  | STAY$_4$ | HF | .09 | .14 | .24 | .13 | .01 | .14 | .07 | .14 | .07 | .14 | .03 | .14 | –.02 | .14 | .07 | .15 | .08 | .15 | .05 | .16 | –.11 | .14 | –.05 | .15 | .08 | .14 |
|  |  | J | .52 | .15 | .68 | .11 | –.05 | .22 | .16 | .20 | .45 | .17 | .22 | .19 | .03 | .19 | .86 | .08 | –.44 | .17 | .38 | .19 | .23 | .18 | .48 | .16 | .60 | .14 |
| RP | M | HF | .18 |  | .27 |  | .17 |  | .09 |  | .13 |  | .15 |  | .10 |  | .09 |  | .03 |  | .00 |  | .13 |  | .09 |  | .03 |  |
|  |  | J | .20 |  | .34 |  | .16 |  | .08 |  | .13 |  | .14 |  | .10 |  | .18 |  | –.04 |  | –.03 |  | .14 |  | .10 |  | .05 |  |
|  | STAY$_2$ | HF | .12 |  | .12 |  | .07 |  | .07 |  | .09 |  | .05 |  | .03 |  | .01 |  | .00 |  | .04 |  | .04 |  | .07 |  | .04 |  |
|  |  | J | .16 |  | .20 |  | .08 |  | .06 |  | .12 |  | .07 |  | .09 |  | .09 |  | –.05 |  | .04 |  | .09 |  | .09 |  | .07 |  |
|  | STAY$_3$ | HF | .09 |  | .10 |  | .06 |  | .06 |  | .08 |  | .04 |  | .03 |  | .00 |  | .00 |  | .03 |  | .03 |  | .05 |  | .03 |  |
|  |  | J | .19 |  | .21 |  | .11 |  | .11 |  | .16 |  | .09 |  | .10 |  | .09 |  | –.05 |  | .08 |  | .09 |  | .12 |  | .10 |  |
|  | STAY$_4$ | HF | .08 |  | .08 |  | .05 |  | .05 |  | .06 |  | .04 |  | .03 |  | .01 |  | .01 |  | .03 |  | .03 |  | .04 |  | .04 |  |
|  |  | J | .17 |  | .18 |  | .08 |  | .08 |  | .14 |  | .05 |  | .09 |  | .10 |  | –.03 |  | .05 |  | .08 |  | .11 |  | .07 |  |
| RGP | STAY$_2$ | HF | –.20 |  | –.05 |  | .06 |  | –.04 |  | –.21 |  | .04 |  | .04 |  | –.05 |  | .22 |  | –.19 |  | –.61 |  | –.04 |  | .19 |  |
|  |  | J | –.36 |  | –.34 |  | –.31 |  | –.75 |  | –.33 |  | .08 |  | .25 |  | .09 |  | .47 |  | –.25 |  | –.76 |  | –.37 |  | –.10 |  |
|  | STAY$_4$ | HF | –.15 |  | –.10 |  | –.19 |  | –.08 |  | –.13 |  | –.14 |  | –.11 |  | –.12 |  | .11 |  | –.03 |  | –.32 |  | –.14 |  | .09 |  |
|  |  | J | .23 |  | .08 |  | .10 |  | .02 |  | .14 |  | .31 |  | .39 |  | .32 |  | –.44 |  | .32 |  | –.16 |  | .32 |  | .53 |  |
| RPP | STAY$_2$ | HF | .06 |  | .04 |  | .02 |  | .04 |  | .05 |  | .01 |  | .00 |  | –.02 |  | –.01 |  | .04 |  | .00 |  | .04 |  | .03 |  |
|  |  | J | .09 |  | .09 |  | .03 |  | .03 |  | .07 |  | .02 |  | .06 |  | .03 |  | –.04 |  | .04 |  | .04 |  | .06 |  | .05 |  |
|  | STAY$_4$ | HF | .04 |  | .02 |  | .01 |  | .03 |  | .03 |  | .01 |  | .01 |  | –.02 |  | .00 |  | .03 |  | .00 |  | .02 |  | .03 |  |
|  |  | J | .12 |  | .09 |  | .04 |  | .06 |  | .10 |  | .01 |  | .07 |  | .05 |  | –.02 |  | .05 |  | .04 |  | .08 |  | .05 |  |

[1] RG = Genetic correlation; RP = phenotypic correlation; RGP = partial genetic correlation after adjustment for first lactation milk, fat, and protein yield; and RPP = partial phenotypic correlation after adjustment for first lactation milk, fat, and protein yield.

[2] All standard errors for phenotypic correlations were ≤.02.

[3] OT = Overall type, DC = dairy character, CAP = capacity, F&L = feet and legs, MAM = mammary system, HGHT = height, ANG = angularity, RLS = rear legs set, FUA = fore udder attachment, RAH = rear attachment height, MSL = medial suspensory ligament, and FTP = fore teat placement.

[4] M = Milk yield, STAY$_i$ = stayability until lactation i.

in value for HF and J (Table 11). The phenotypic correlation was highest between dairy character and milk yield; estimates were .27 and .34 for HF and J. Genetically, dairy character was most highly correlated with first lactation milk yield; estimates for the genetic correlation were .50 and .84 for HF and J. Each of the summary traits, for which higher scores were more desirable, was positively correlated with milk yield in HF and J. Genetic correlations between the type traits of size and height (traits most likely to be correlated with body weight) and milk yield were not significantly different from zero. The phenotypic correlation between size and milk yield was .10 for HF and J data (Table 11).

Phenotypic correlations between stayabilities and type traits generally were low; correlations were slightly higher for J (Table 11). The largest phenotypic correlation between $STAY_4$ and type traits was .08 for overall type for HF and .18 for dairy character for J. Genetic correlations between type traits and stayabilities were low, although standard errors were large. For J, overall type, dairy character, and angularity were highly correlated with stayability scores, but this correlation may be an indirect effect of the high genetic correlation between stayabilities and yield of J (see Table 8). This explanation may also apply to the moderate correlation between stayabilities and overall type and dairy character for HF data.

Despite large amounts of data on type traits worldwide, several authors (4, 5, 7, 10, 24) have noted that no consistency exists among breeds and subpopulations within breeds in which type traits are important for prediction of survival traits. This could be because of the large standard errors usually associated with these estimates, or to varying biases between studies, or to real differences between studies for the true genetic correlations.

Using the phenotypic covariance matrix from Table 11, the proportion of variance in stayabilities explained by yield and type traits ($R^2$) was calculated to be .11 and .13 for $STAY_2$ for HF and J, respectively. For $STAY_4$ these values reduced to .10 and .05 (Table 11). When the genetic covariance matrix was used, the $R^2$ were much higher, .87 and .92 for HF and J for $STAY_2$.

After adjustment for milk, fat, and protein yield, partial phenotypic correlations between stayabilities and type traits were even lower, and $R^2$ were close to zero (Table 11). Genetically, partial correlations between type traits and stayabilities were negative for most type traits.

Given the correlations between many type traits and stayability, it may appear logical to use type traits in a multiple regression equation to predict stayability. However, the sampling errors associated with estimates of genetic (co)variances cause the $R^2$ value for these multiple regressions to be overestimated (26, 31).

Using the correlations between type traits and $STAY_4$ from Table 11 in a multiple genetic regression of $STAY_4$ on all 13 type traits gave an $R^2$ of .70 and 1.00 for prediction of $STAY_4$ from type traits for HF and J, respectively. However, part of the information for prediction of stayability comes from the correlation between type traits and yield traits. When the correlations between type traits and stayability were adjusted by a genetic regression on milk, fat, and protein yield, the $R^2$ were .57 and 1.00 for HF and J (Table 11). Both of these $R^2$ values were likely overestimated, and the overestimation should have been greater in the J because the sampling errors of the covariances were greater for J. By comparison, a phenotypic multiple regression of $STAY_4$ on type traits, calculated from the phenotypic correlations in Tables 10 and 11, which have low standard errors, had an $R^2$ of .05 for HF. When the phenotypic regressions were corrected for the effect of milk, fat, and protein yields, the $R^2$ dropped to .004 in HF. These phenotypic $R^2$ are comparable with those reported by Beard and Jones (2) for Australian cattle. Results from the US show a similar pattern. Boldman et al. (3) reported a genetic $R^2$ of .56 for predicting functional herd life from 18 type traits. With less accurate estimates of genetic parameters, Harris et al. (10) estimated a genetic $R^2$ of .99 for US Guernseys. However, at the phenotypic level, Burke and Funk (6) found that 14 type traits explained .14 of the variation in herd life for US Holsteins.

Caution should be exercised in using a combination of type traits to predict breeding values for herd life because the genetic multiple $R^2$ would likely be overestimates, because the estimates of phenotypic $R^2$ are much lower than the estimates of genetic $R^2$, and because

TABLE 12. Heritability estimates from analyses for Holstein-Friesian (HF) and Jersey (J) cattle.

| | | HF | | J | |
|---|---|---|---|---|---|
| Trait[1] | Analysis[2] | $h^2$ | SE[3] of $h^2$ | $h^2$ | SE of $h^2$ |
| M | 2a | .24 | .02 | .28 | .04 |
| | 2b | .16 | .03 | .24 | .06 |
| | 3 | .20 | .03 | .30 | .07 |
| | 4 | .19 | .03 | .38 | .10 |
| $STAY_2$ | 1 | .03 | .00 | .07 | .01 |
| | 2a | .05 | .01 | .07 | .02 |
| | 2b | .05 | .01 | .22 | .06 |
| | 3 | .01 | .00 | .04 | .01 |
| | 4 | .03 | .01 | .07 | .02 |

[1] M = First lactation milk yield; $STAY_2$ = stayability until lactation 2.

[2] 1 = Survival (milk yield not analyzed), 2 = production and stayability for opportunity group until lactation 2 (2a) or until lactation 6 (2b), 3 = production and workability, and 4 = production and type.

[3] Standard error of .00 means <.005.

results of the type traits that predict herd life are not consistent.

### Selection Bias

The methods of data selection and analysis may have caused biases in parameter estimates because the sires in the analyses may have been a selected group. Data for the survival analyses were for sires with the largest progeny groups. Hence, sires represented in the survival analyses were likely to be a biased sample with respect to yield traits and traits correlated with yield. For analysis of workability and yield and for type and yield, all sires were treated as random effects. For the older age groups, the sires represented may have been a selected group, and so results may be biased slightly. For all analyses, selection of the parents of the bulls was only (partly) taken into account if their sires had daughters with records in the data, which was the case for some younger bulls, but not for the older ones.

The heritability estimate for first lactation milk yield and $STAY_2$ from different analyses are presented in Table 12. The results from the analyses using only first lactation records should have little bias. For HF, the estimates are as expected if selection biases existed; highest (.24 and .05 for milk yield and $STAY_2$, respectively) for the analysis of first lactation data, and lower for all other analyses. However, differences across analyses were relatively small. For J the results are less clear, possibly because of large sampling errors. The level of bias appears acceptable in return for greater precision, which is needed especially for the estimates of genetic correlations.

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