Genotype by Environment Interaction for Fertility, Survival, and Milk Production Traits in Australian Dairy Cattle

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ABSTRACT

The existence of a genotype $\times$ environment interaction ($G \times E$) for fertility traits, survival, and milk yield traits was examined by considering performance recorded in different calving systems (seasonal, split, and year round) or regions as different traits. For fertility traits and survival, $G \times E$ were also investigated by applying a random regression model using continuous environmental variables, such as level of herd milk production, temperature-humidity index, and herd size as environmental descriptors. The traits considered were calving interval, calving to first service interval (CFS), 25-d nonreturn rate at first service, pregnancy rate, survival, milk yield, fat yield, and protein yield and percentage. Data on Holstein-Friesian cows that calved between 1997 and 2005 were analyzed. The number of cows included in the analyses ranged from approximately 21,000 for pregnancy rate to approximately one-half million for survival. For all traits, heterogeneity in additive and phenotypic variances was observed. For example, for CFS the additive genetic and phenotypic variance in seasonal calving herds was only 9 and 15% of that in year-round calving herds, respectively. Genetic correlations among calving systems for milk yield traits were greater than 0.96. For calving interval, the lowest genetic correlation, of 0.83, was between split and year-round calving herds, but for CFS and pregnancy rate, genetic correlations as low as 0.37 were observed, although these estimates were associated with large standard errors. Genetic correlations between traits recorded in different Australian regions were greater than 0.89. Heritability and phenotypic variance for milk yield traits were the greatest in region 1, which consisted of Queensland, West Australia, South Australia, and New South Wales, and were least in region 3, which included Gippsland and Tasmania, in accordance with mean

milk yield levels. Genetic correlations as low as 0.5 for some fertility traits between the 5th and 95th percentile of the distribution of the environmental descriptors, such as herd size and average herd milk production, were also observed. However, these estimates had large standard errors. Regardless of the environmental descriptor used, there was no evidence for the presence of a large $G \times E$ that resulted in economically significant reranking of bulls.

Key words: genotype $\times$ environment interaction, fertility, milk production, survival

INTRODUCTION

The main goal of a national genetic evaluation system is to identify sires that are consistently superior across all environments for all economic traits. A recent analysis of Australian dairy cattle milk production data showed that bull reranking was significant but small for milk yield traits when environments were defined by environmental descriptors such as herd size, average herd test-day protein yield, temperature-humidity index (THI), and herd test-day coefficient of variation for protein yield (Hayes et al., 2003). Only a small amount of reranking was observed in the Netherlands for milk yield traits (Calus and Veerkamp, 2003), where environments were defined as herd-year average protein yield, BCS, or age at calving. Kearney et al. (2004a), working with US data, did not find evidence for a genotype $\times$ environment interaction ($G \times E$) after comparing 2 management systems (grazing vs. confinement). However, there has been little examination of a $G \times E$ for fertility traits. The few studies that have investigated a $G \times E$ for fertility traits have reported slightly lower genetic correlations (i.e., more $G \times E$) between different environments for fertility traits than for milk yield traits (Boettcher et al., 2003; Kearney et al., 2004b). In general, genetic correlations between environments are lower for functional traits than for milk production traits. For example, the average genetic correlation for longevity in different Interbull member countries is approximately 0.59, compared with approximately 0.88 for milk yield traits (Mark, 2004).

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Dairy farming in Australia varies in many ways, including the level of feeding, geographic regions, herd size, intensity of production, calving system, and climatic variables, such as temperature and humidity. The diverse production environments suggest that the magnitude of $G \times E$ could be high, in particular for traits such as fertility, which are directly influenced by calving pattern and climatic conditions. Thus, when investigating the importance of a $G \times E$ for fertility, environmental descriptors such as differences in geographical regions, climate, and calving system (seasonal vs. year-round calving herds) should be considered.

The THI is considered to have an important effect on milk and fertility traits in dairy cattle in Australia (Mayer et al., 1999; Morton et al., 2007). Hayes et al. (2003) observed a $G \times E$ for fat yield across THI, with a genetic correlation of 0.90 between fat yield at the 5th and 95th percentile of THI. Ravagnolo and Misztal (2002) noted heat stress measured as THI to be relatively more important on nonreturn rate (NRR) than on milk yield traits. In southeastern Australia, where most of the dairy farming is practiced, most cows are mated during the hot summer months (October to January) and calve by the end of the winter (July to September). The effect of heat stress on the fertility level of dairy cows is well documented (Morton et al., 2007), but very little is known about genetic differences in the response to heat stress (Ravagnolo and Misztal, 2002).

Until recently, most studies have investigated $G \times E$ by categorizing performances observed in different environments or management systems as different traits, and then calculating genetic correlations between these traits (Kearney et al., 2004a). In Australia, there is a general expectation that the interaction between genotype and calving system or geographical region is important (Paine and Alexander, 2007; Fulkerson et al., 2008). To the present, however, the extent of these has not been documented for any trait. An alternative to partitioning the environments into classes is to consider the environmental descriptor as a continuous variable in a random regression (RR) model. Many environmental descriptors that influence the performance of cows, such as concentrate feeding level (indicated by herd production level), herd size, and climate, have continuous distributions.

The main objective of this study was to assess the magnitude of a $G \times E$ on fertility traits [calving interval, calving to first service interval (CFS), first service NRR, pregnancy rate] and survival for a range of environmental descriptors. The environmental descriptors considered were herd size, average herd lactation milk yield (AHLMY), THI, calving system, and geographical region. Evidence for genotype $\times$ calving system and

geographical region was also investigated for milk yield traits. Both multitrait and RR approaches were used to calculate genetic correlations of fertility traits between extremes of environmental descriptors that were distinct (calving system, region) or continuous (herd average production level, herd size, and THI).

MATERIALS AND METHODS

Traits

To achieve the objectives of this study, the following fertility traits and survival data were analyzed: calving interval (CI), CFS, pregnancy rate, 25-d NRR at first service, and survival (survival to the next lactation). The NRR was coded as 100 if a cow was inseminated and observed for at least 25 d after the first insemination and no other insemination was recorded, and 0 otherwise. Cows that were not inseminated at all and those observed for less than 25 d were coded as missing. Cows were considered pregnant and coded as 100 if the age of the fetus at pregnancy diagnosis was at least 30 d, and 0 otherwise. If the age of the fetus was less than 30 d, cows were coded missing. In the case of survival, cows with a known next calving date were coded as 1. A cow was coded 0 if the herd to which she belonged had continued milk recording and the cow herself did not have a test or calving record for at least 18 mo after her previous calving. Survival was coded missing if the fate of the cow could not be determined. Cows with a CI between 300 and 730 d and with CFS between 15 and 250 d were accepted as valid records. The presence of a genotype $\times$ region or calving system interaction was tested for 305-d milk yield, protein yield, fat yield, and protein percentage. Mean, standard deviation, and number of records for the traits considered in this study by calving system are given in Table 1. For most traits, the data used for this study were from 5,665 herds. However, only approximately one-third of the herds provided mating or pregnancy data.

Data

Calving, survival, and mating data of Holstein-Friesian (HF) cows were extracted from the Australian Dairy Herd Improvement Scheme (ADHIS) database. Herds with at least 90 calving records between January 1997 and December 2005 were selected. Only HF cows that had HF breed as both sire and dam breed were included in this study. Only cows sired by bulls in an AI program with at least 5 progeny in the original data set were included in this study. Only herd-year-seasons of calving (HYS) with more than 3 cows were included. For this study, first-parity cows that had calved between

Table 1. Mean and standard deviation for calving interval (CI), calving to first service interval (CFS), first service nonreturn rate (NRR), pregnancy, survival, and 305-d milk yield, fat and protein yield in seasonal, split, and year-round calving herds

Trait	Seasonal			Split			Year round		
	Mean	SD	n ¹	Mean	SD	n ¹	Mean	SD	n ¹
CI, d	396	77	210,446	415	87	34,196	421	82	138,362
CFS, ² d	82	25	82,143	89	36	21,362	102	48	9,896
NRR, ² %	56.2	49.6	64,763	54.9	49.8	17,402	55.8	49.7	9,312
Pregnancy, ² %	80.4	39.7	20,478	76.4	42.5	11,816	85.0	35.7	3,845
Survival, %	84.0	36.7	264,972	83.5	37.1	46,058	82.0	38.4	171,023
Milk yield, kg	5,270	1,301	243,203	5,808	1,417	43,710	5,966	1,405	158,106
Fat yield, kg	202	46.8	243,203	219	51.4	43,710	224	54.8	158,106
Protein yield, kg	168	42.3	243,203	186	46.4	43,710	187	45.4	158,106

¹Number of cows with a valid record.

²Data from the first 5 parities were used for these traits; for other traits, only the first-parity data were used.

18 and 37 mo of age were selected. For most traits, only data recorded during the first lactation of the cow were analyzed, but because the number of first-parity cows with pregnancy rate, CFS, and NRR data was small, data on the first 5 parities were used.

All the available pedigree data of sires of the cows with records and their ancestors as far back as 1950 were included. The number of sires with progeny varied from 1,902 for the pregnancy test data to 7,611 for survival.

Environmental Descriptors

Two distinct environmental descriptors (calving system and geographic region) and 3 continuous environmental descriptors (AHLMY, herd size, and THI) were considered in the current study. Data from 5,665 herds were classified into seasonal (once per year), split (twice per year), and year-round calving herds based on their calving, mating, and pregnancy test data (Table 1). Split calving is an intermediate system between seasonal and year-round calving systems. Figure 1 highlights the proportion of cows that calved in each month of the year for the 3 calving systems. The routine that

classified herds into calving systems was jointly developed by the InCalf project (<http://www.incalf.com.au>), ADHIS (<http://www.adhis.com.au>), and Gippsland Herd Improvement (<http://www.gippslandhi.coop>) as a tool for fertility management. Based on this routine, 55, 36, and 9% of the records were classified as seasonal, year-round, and split calving herds. In 94% of the cases, herds were classified into the same system of calving for the whole study period (1997 to 2005).

Herds were also divided into 3 regions, which differed in a combination of factors, including geographical location, milk production and fertility level, and purpose of milk production (Table 2). Region 1 included largely fluid milk-producing, low-fertility (long CI), and relatively warm-climate, year-round calving herds from New South Wales, West Australia, Queensland, and South Australia. Data from north and west Victoria formed the second group (region 2), and herds from Gippsland and Tasmania formed the third group (region 3). The second and the third groups are manufacturing milk-producing regions with relatively better fertility but with different levels of milk production. The majority of the herds that formed regions 2 and 3 were seasonal or split calving herds. Table 3 shows the fraction of

Table 2. Trait means and descriptive features of groups formed by a combination of criteria such as geographical location or climatic condition, milk production, fertility and production objective (fluid or manufacturing milk production)

Region, state ¹ (region no.)	305-d milk yield, kg	Calving interval, d	Calving to first service, d	Survival, %	305-d protein, %	305-d fat yield, kg	Production system features
QLD, NSW, WA, SA (1)	6,006	418 (148,032) ²	97.3	82.5	3.13	224.8	Fluid milk, year round, warmer
North and West Victoria (2)	5,572	400 (127,552)	83.8	84.1	3.20	211.4	Manufacturing milk, split or seasonal, milder
Gippsland, Tasmania (3)	4,993	399 (107,420)	82.6	83.2	3.20	194.6	Manufacturing milk, seasonal, cool

¹QLD = Queensland; NSW = New South Wales; WA = West Australia; SA = South Australia.

²Numbers in parentheses are cows with a valid record.

Figure 1. Proportion of cows that calved in each month of the year in year-round, seasonal, and split calving herds.

herds in each calving system and region. The classification of herds into regions was largely subjective but was designed to investigate a possible $G \times E$ between fluid milk-producing versus manufacturing milk-producing systems as well as geographical regions.

Environmental descriptors such as AHLMY and herd size were based on all cows that calved and produced in the herd in a particular year. The AHLMY were calculated after adjusting records for age and DIM according to the ADHIS procedure, based on the production of all cows in the herd. Table 4 shows the mean, minimum, and maximum values for the continuous environmental descriptors. The THI recorded on the day of insemination was used as an environmental descriptor for NRR

only. Earlier studies (Ravagnolo and Misztal, 2002; Morton et al., 2007) and preliminary analyses based on the current data have shown that THI on the day of mating is more important for NRR than THI before or after the mating day. The source of the climate data used and a detailed formula for calculating THI are given by Hayes et al. (2003). In short, THI is derived from the dry-bulb temperature (T_{db}) and the dew-point temperature (T_{dp}) as follows: $THI = T_{db} + 0.36 \times T_{dp} + 41.2$.

Data Analyses

All statistical analyses were performed by using AS-REML (Gilmour et al., 2006).

Table 3. Number of year-round, seasonal and split calving herds from the regions of Australia¹

Region	Calving system			Total
	Seasonal	Split	Year round	
1	0.13 ² (0.08) ³	0.05 (0.20)	0.82 (0.88)	1,721
2	0.84 (0.52)	0.10 (0.51)	0.06 (0.06)	1,825
3	0.85 (0.40)	0.08 (0.29)	0.07 (0.06)	2,119
Total	3,291	501	1,873	5,665

¹Region 1 = New South Wales, Queensland, South and West Australia; region 2 = North and West Victoria; region 3 = Gippsland, Tasmania.

²Values within a row are the fraction of herds in a region from each calving system.

³Values within a column (in parentheses) are the fraction of herds in a calving system from each region.

Table 4. Mean, standard deviation, and range for continuous environmental descriptors used

Environmental descriptor	Mean	SD	Minimum	Maximum
Herd lactation milk yield, kg	6,257	1,168	2,636	10,000
Herd size	288	151	30	1,000
Temperature-humidity index	63.5	7.3	40	90

Distinct Environmental Descriptors. For examining a genotype $\times$ calving system or region interaction, the performance of cows in each calving system or region were considered as different traits. Thus, the following multiple-trait sire model, which considered the performance of daughters in the 3 calving systems or regions as different correlated traits, was fitted:

$$Y_{ijklmn} = \mu_t + \text{HYS}_{ti} + M_{tk} + \{P_{il}\} + \sum_{o=1}^2 B_{to} \text{Age}_{tmo} + \text{Sire}_{tm} + \{\text{Cow}_{ij}\} + e_{ijklmn}, \quad [1]$$

where Y_{ijklmn} is the n th observation; μ_t is the overall mean for the t th trait (calving system or region); HYS_{ti} is the fixed effect of the i th HYS (2 seasons of 6 mo each) of calving for the t th trait; M_{tk} is the fixed effect of the k th month of calving for the t th trait; $\{P_{il}\}$ is the fixed effect of the l th parity for the t th trait; Age_{tmo} is the second-order polynomial corresponding to age at calving (in months) for the t th trait; B_{to} is the regression coefficient (linear and quadratic) of age on the t th trait; Sire_{tm} is the random effect of the m th sire for the t th trait; $\{\text{Cow}_{ij}\}$ is the random permanent environmental effect of the j th cow for the t th trait; and e_{ijklmn} is the random residual term. Terms in braces (parity and permanent environmental effect of the cow) are fitted only for CFS, NRR, and pregnancy rate where repeated records are used.

The covariance structure for model 1, in which records in different calving systems or regions are considered as different traits is

$$\text{Var} \begin{pmatrix} s1 \\ s2 \\ s3 \end{pmatrix} = \begin{pmatrix} A\sigma^2 s1 & A\sigma s1, s2 & A\sigma s1, s3 \\ A\sigma s1, s2 & A\sigma^2 s2 & A\sigma s2, s3 \\ A\sigma s1, s3 & A\sigma s2, s3 & A\sigma^2 s3 \end{pmatrix},$$

$$\text{Var} \begin{pmatrix} e1 \\ e2 \\ e3 \end{pmatrix} = \begin{pmatrix} \sigma^2 e1 & 0 & 0 \\ 0 & \sigma^2 e2 & 0 \\ 0 & 0 & \sigma^2 e3 \end{pmatrix},$$

where $s1$, $s2$, and $s3$ represent the sire effect of cows with performance recorded in 1 (seasonal calving system or region 1), 2 (split calving system or region 2), and 3 (year-round calving system or region 3), respectively, $\mathbf{A}$ is the genetic relationship matrix among sires and their ancestors; and $\sigma^2 s1$, $s2$, $\sigma^2 s3$, $\sigma s1$, $\sigma s2$, and so on represent the sire genetic (co)variances of traits recorded in the different calving systems or regions. For pregnancy rate, CFS and NRR, where repeated records of cows are considered the permanent environmental covariance matrix, were modeled as $\mathbf{I} \otimes \mathbf{P}$, where $\mathbf{I}$ is an identity matrix, $\otimes$ is the Kronecker product, and $\text{Var}(\mathbf{P}) = \text{diag}\{\sigma^2 p1 \sigma^2 p2 \sigma^2 p3\}$. Both the permanent

environmental and residual covariances were not estimable and thus were set to be zero, because cows performed in one environment only.

To facilitate convergence, results from a univariate analysis and bivariate analyses were used as the starting value for the trivariate analyses. In the case of NRR, CFS, and pregnancy rate, the trivariate analyses did not converge, so results from a set of bivariate analyses were tabulated. To test the significance of a $G \times E$ between calving systems or regions, the likelihood ratio test was used by comparing the log-likelihood of a full model against a model in which the genetic correlations between calving systems or regions were fixed at unity. A chi-square test with 2 degrees of freedom was used to test for the significance of a $G \times E$.

Furthermore, the genetic correlations between CI and milk yield in seasonal and year-round calving herds in a 4-trait analysis (two CI and two 305-d milk yields in seasonal and year-round calving herds) were estimated to examine whether the level of genetic antagonism between fertility and milk yield was influenced by calving system. Model 1 was used for this analysis, and the covariance structure, where records of milk yield and CI in the 2 calving systems are considered as different traits, is given below:

$$\text{Var} \begin{pmatrix} s1 \\ s2 \\ s3 \\ s4 \end{pmatrix} = \begin{pmatrix} A\sigma^2 s1 & A\sigma s1, s2 & A\sigma s1, s3 & A\sigma s1, s4 \\ A\sigma s1, s2 & A\sigma^2 s2 & A\sigma s2, s3 & A\sigma s2, s4 \\ A\sigma s1, s3 & A\sigma s2, s3 & A\sigma^2 s3 & A\sigma s3, s4 \\ A\sigma s1, s4 & A\sigma s2, s4 & A\sigma s3, s4 & A\sigma^2 s4 \end{pmatrix},$$

$$\text{Var} \begin{pmatrix} e1 \\ e2 \\ e3 \\ e4 \end{pmatrix} = \begin{bmatrix} \sigma^2 e1 & 0 & \sigma e1, e3 & 0 \\ 0 & \sigma^2 e2 & 0 & \sigma e2, e4 \\ \sigma e1, e3 & 0 & \sigma^2 e3 & 0 \\ 0 & \sigma e2, e4 & 0 & \sigma^2 e4 \end{bmatrix},$$

where $s1$, $s2$, $s3$, and $s4$ represent the sire effect of cows with milk yield records in seasonal and year-round calving systems, and represent CI in seasonal and year-round calving systems, respectively; $\mathbf{A}$ is as defined earlier; and $\sigma^2 s1$, $\sigma^2 s2$, $\sigma^2 s3$, ... $\sigma s1$, $s2$, and so on represent the sire genetic (co)variances of the 2 traits recorded in seasonal and year-round calving systems. Residual covariances are defined only for milk yield and CI when recorded in the same calving system.

Continuous Environmental Descriptors. First-parity fertility data were analyzed to investigate whether the response of daughters of sires was influenced by the environmental variables in which they performed by using the following RR model:

$$Y_{ijlm} = \mu + \text{HYS}_i + M_j + \sum_{n=1}^2 B_n \text{Age}_{mn} + \sum_{n=1}^6 D_n Z_{mn} + \sum_{n=0}^2 S_{ln} Z_{mn} + e_{ijlm}, \quad [2]$$

where Y_{ijlm} is an observation; μ is the overall mean; HYS_i is the effect of the i th HYS of calving; M_j is the effect of the j th month of calving; B_n is a fixed regression coefficient of age at calving; Age_{mn} is the second-order orthogonal polynomial corresponding to the m th age of calving; D_n is a fixed regression coefficient of the environmental descriptor; Z_{mn} is the n th-order orthogonal polynomial corresponding to the level of the environmental descriptor on the m th record; S_{ln} is an RR coefficient of environmental descriptor times the l th sire with a numerator relationship; and e_{ijlm} is a random residual effect assumed to have the same (co)-variance matrix for a group of records formed based on the environmental descriptor but allowed to vary across groups.

The (co)variance structure for model 2 is

$$\text{Var}(\mathbf{S}) = \begin{pmatrix} s0 \\ s1 \\ s2 \end{pmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2 s0 & \mathbf{A}\sigma s0, s1 & \mathbf{A}\sigma s0, s2 \\ \mathbf{A}\sigma s0, s1 & \mathbf{A}\sigma^2 s1 & \mathbf{A}\sigma s1, s2 \\ \mathbf{A}\sigma s0, s2 & \mathbf{A}\sigma s1, s2 & \mathbf{A}\sigma^2 s2 \end{bmatrix},$$

$$\text{Var}(\mathbf{e}) = \mathbf{R} = \text{diag}\{\mathbf{I}_{n1}\sigma^2 e1 \mathbf{I}_{n2}\sigma^2 e2 \dots \mathbf{I}_{n10}\sigma^2 e10\}.$$

Regardless of the environmental descriptor, 10 equally sized groups were formed for all traits based on increasing environmental descriptors to include heterogeneous residual variances in the model. In all cases, residual covariances were set to zero. In the case of NRR and survival (coded as 100 or 0), only one residual variance was fitted because estimates of residual variances were converging to zero when more than one residual variance was fitted. The order of the polynomials for the fixed regression for environmental descriptors was set to 6 in each situation. The fixed regression on environmental descriptors was included to account for the average effect across the environmental variable (Calus and Veerkamp, 2003). For the RR component, a polynomial fit of first (i.e., intercept and linear) or second (i.e., intercept, linear, and quadratic) order were tested based on log-likelihood tests. Except in the case of NRR and survival, the order was set to 3 in the final analyses based on log-likelihood tests. In the case of NRR and survival, analysis results from a polynomial order of 2 are presented because analyses in which the order of the polynomial was set to 3 did not converge. When herd size was considered as an environmental descriptor in the case of survival, only the model with an intercept converged.

Calculation of Genetic Parameters. The sire variances for values of environmental descriptors are calculated as $\Phi \text{Var}(\mathbf{S}) \Phi'$, where Φ is a matrix with polynomial coefficients for a value of the environmental descriptor in each row and $\text{Var}(\mathbf{S})$ is a 3×3 matrix with variances of each RR coefficient on the diagonal and with covariances between the RR coefficients on the off-diagonals. The presence of $G \times E$ for fertility traits was assessed by calculating heritabilities and genetic correlations at the 5th, 50th, and 95th percentiles of the environmental variables. Heritabilities were calculated as the ratio of 4 times the sire variance divided by the sum of sires and the residual variance for the appropriate group. Genetic correlations were estimated as the ratio of the sire covariance between 2 environmental variables (e.g., the 5th and 50th percentiles) to the square root of the sire variance in each environmental variable (e.g., the 5th and 50th percentiles).

RESULTS

Distinct Environmental Descriptors

Genotype × Calving System Interaction. The number of records in Table 1 for each trait shows that the largest amounts of the data were from seasonal calving herds, followed by year-round calving herds for most traits. However, for some fertility traits that

Table 5. Estimated phenotypic variance, heritability (on diagonal), and genetic correlation (below diagonal) for calving systems for calving interval, calving to first service, first service nonreturn rate, survival, pregnancy rate, and 305-d milk, fat and protein yield

System	Phenotypic σ^2	Seasonal	Split	Year round
Calving interval				
Seasonal	4,312	0.02 ± 0.0^3		
Split	5,787	0.89 ± 0.07^4	0.03 ± 0.01	
Year round	5,805	0.96 ± 0.04	0.83 ± 0.09^4	0.03 ± 0.0^3
Calving to first service ^{1,2}				
Seasonal	223	0.02 ± 0.0^3		
Split	729	0.77 ± 0.11^4	0.03 ± 0.01	
Year round	1,448	0.93 ± 0.10	0.99 ± 0.12	0.03 ± 0.01
First service nonreturn rate ^{1,2}				
Seasonal	2,105	0.01 ± 0.0^3		
Split	2,131	0.99 ± 0.0^3	0.01 ± 0.0^3	
Year round	2,259	0.99 ± 0.0^3	0.99 ± 0.0^3	0.01 ± 0.0^3
Pregnancy rate ^{1,2}				
Seasonal	926	0.01 ± 0.01		
Split	1,077	0.83 ± 0.54	0.01 ± 0.01	
Year round	817	0.99 ± 0.0^3	0.37 ± 1.53	0.01 ± 0.01
Survival				
Seasonal	1,200	0.03 ± 0.0^3		
Split	1,222	0.99 ± 0.0^3	0.04 ± 0.01	
Year round	1,383	0.96 ± 0.03	0.91 ± 0.06	0.03 ± 0.0^3
305-d milk yield				
Seasonal	601,900	0.28 ± 0.01		
Split	824,800	0.99 ± 0.01	0.25 ± 0.02	
Year round	824,100	0.98 ± 0.01	0.98 ± 0.01	0.29 ± 0.01
305-d protein yield				
Seasonal	542	0.23 ± 0.01		
Split	772	0.98 ± 0.01	0.21 ± 0.01	
Year round	738	0.97 ± 0.01	0.97 ± 0.01	0.23 ± 0.01
305-d fat yield				
Seasonal	875	0.22 ± 0.01		
Split	1,204	0.99 ± 0.01	0.21 ± 0.01	
Year round	1,229	0.97 ± 0.01	0.97 ± 0.01	0.24 ± 0.01

¹Results are based on data in the first 5 parities.

²Results are based on a set of bivariate analyses because trivariate analyses did not converge.

³Standard error of the estimates rounded to zero.

⁴A chi-square test with 2 degrees of freedom conducted by comparing the likelihood ratio of a full model against a model in which the correlation was fixed at unity showed significance at an 0.05 probability level.

needed special attention to record, such as pregnancy rate, CFS, and NRR, the numbers of records from year-round calving herds were smaller than from split calving herds (Table 1). Table 1 shows that mean CI, CFS, milk yield, fat yield, and protein yield were the lowest in seasonal calving herds and greatest in year-round calving herds. Variations in unadjusted mean value for traits such as NRR and survival between calving systems were small (Table 1).

Heritability estimates for all traits did not differ because of calving system (Table 5). For pregnancy rate, CFS, and NRR, where data from the first 5 parities were used, the ratio of cow variance to total phenotypic variance varied from 0.03 to 0.05. For CFS and pregnancy rate, genetic correlations between split and seasonal calving herds were relatively low (Table 5), but these estimates were associated with high standard errors. In particular, the standard error of the genetic

correlation estimate for pregnancy rate between split and year-round calving herds was high (Table 5) because the number of sires with at least 2 progeny in year-round calving herds was small (440) and only approximately half (225) of them had at least 2 progeny in split calving herds as well. Estimates based on CI also showed genetic correlations of below 0.9 between split and year-round calving herds (Table 5).

For both milk yield traits and CI, all genetic correlations were above 0.8, suggesting little genotype $\times$ calving system interaction (Table 5). As expected from this correlation, most of the bulls ranked similarly in the 3 calving systems. Figures 2 and 3 illustrate solutions for 7 bulls that showed the most change in progeny-transmitting ability (based on the sum of absolute difference of bull solutions in the 3 calving systems) for protein yield and CI. The 7 bulls were selected from 414 bulls with at least 100 daughters for protein yield

Figure 2. Solutions for bulls with more than 100 progeny across the 3 calving systems for protein yield.

and 272 bulls with 200 daughters for CI. These results show that there were a few apparently environmentally sensitive bulls.

For traits such as milk yield, CI, and CFS, the phenotypic and genetic variances were influenced by calving system (Table 5). The CFS was the most extreme trait, in which case the additive genetic variance and total phenotypic variance in seasonal calving herds was only 9 and 15% of that in year-round calving herds, respectively.

Table 6 shows the total phenotypic variance, heritability, and correlations for 305-d milk yield and CI for the 2 most important calving systems (seasonal and year round) and the degree of genetic antagonism between 305-d milk yield and CI. The genetic correlations between CI in seasonal and year-round calving herds as well as between 305-d milk yield in the 2 calving systems were similar to those shown in Table 5, and the genetic antagonism between fertility and milk production did not appear to be influenced by calving system.

Figure 3. Solutions for bulls with more than 200 progeny across the 3 calving systems for calving interval.

Table 6. Heritability (on diagonal), genetic (below diagonal), and residual correlation (above diagonal) for calving interval and 305-d milk yield in seasonal and year-round calving systems

Trait	Calving system	305-d milk yield		Calving interval	
		Seasonal	Year-round	Seasonal	Year-round
305-d milk yield	Seasonal	0.26 ± 0.01 (656,700) ²	0 ¹	0.13 ± 0.0 ³	0 ¹
	Year round	0.97 ± 0.01	0.26 ± 0.01 (820,000) ²	0 ¹	0.16 ± 0.0 ³
Calving interval	Seasonal	0.39 ± 0.06	0.46 ± 0.06	0.02 ± 0.0 ³ (4,264) ²	0 ¹
	Year round	0.32 ± 0.06	0.36 ± 0.06	0.98 ± 0.03	0.03 ± 0.0 ³ (5,807) ²

¹Residual correlation not defined.²Phenotypic variances estimates are in parentheses.³Standard error of the estimates rounded to zero.

Genotype × Region Interaction. Table 2 shows the unadjusted mean value for each trait analyzed for the 3 regions. The mean CI, CFS, 305-d milk yield, and 305-d fat yield were the lowest for region 3, which is characterized as a seasonal calving, low-input, and cool-climate region producing milk mainly for manufacturing purposes. Table 7 shows estimated heritabilities and genetic correlations between regions for CI, CFS, survival, and 305-d milk yield, fat yield, and protein percentage. Heritabilities for CFS and 305-d milk yield were the greatest in region 1, where milk yield levels

were the greatest. The lowest genetic correlation, of 0.81, was observed between region 2 and 3 for CFS. Very high genetic correlations close to unity were estimated for protein percentage (a highly heritable trait) between regions.

Genotype × Continuous Environmental Descriptors Interaction

Mean values of environmental descriptors, heritability estimates, mean values of the traits, and genetic

Table 7. Estimated phenotypic variance, heritability (on diagonal), and genetic correlation (below diagonal) for regions for calving interval, calving to first service, survival, 305-d milk yield, 305-d fat yield, and 305-d protein percentage

Region ¹	Phenotypic σ^2	Region 1	Region 2	Region 3
Calving interval				
Region 1	5,620	0.03 ± 0.0 ³		
Region 2	4,567	0.97 ± 0.04	0.02 ± 0.0 ³	
Region 3	4,815	0.96 ± 0.04	0.99 ± 0.04	0.03 ± 0.0 ³
Calving to first service ²				
Region 1	1,290	0.04 ± 0.01		
Region 2	415	0.83 ± 0.11	0.02 ± 0.0 ³	
Region 3	263	0.89 ± 0.08	0.8 ± 0.10	0.02 ± 0.0 ³
Survival				
Region 1	1,349	0.04 ± 0.0 ³		
Region 2	1,187	0.98 ± 0.03	0.03 ± 0.0 ³	
Region 3	1,254	0.91 ± 0.05	0.98 ± 0.03	0.04 ± 0.01
305-d milk yield				
Region 1	820,000	0.31 ± 0.01		
Region 2	689,800	0.99 ± 0.01	0.28 ± 0.01	
Region 3	564,300	0.94 ± 0.01 ⁴	0.97 ± 0.01	0.25 ± 0.01
305-d fat yield				
Region 1	1,216	0.25 ± 0.01		
Region 2	977	0.97 ± 0.01	0.21 ± 0.01	
Region 3	856	0.90 ± 0.02 ⁴	0.94 ± 0.01 ⁴	0.22 ± 0.01
305-d protein %				
Region 1	308	0.58 ± 0.01		
Region 2	350	0.99 ± 0.01	0.55 ± 0.01	
Region 3	314	0.99 ± 0.01	0.99 ± 0.01	0.57 ± 0.02

¹Region 1 includes high milk yield, long calving interval, warmer climate fluid milk-producing region (New South Wales, Queensland, South and West Australia); region 2 includes medium milk yield, short calving interval, manufacturing milk-producing region (North and West Victoria), region 3 is low milk yield, short calving interval, cool-climate manufacturing milk-producing region (Gippsland and Tasmania).

²Results are based on data in the first 5 parities.

³Standard error of the estimates rounded to zero.

⁴A chi-square test with 2 degrees of freedom conducted by comparing the likelihood ratio of a full model against a model in which the correlation was fixed at unity showed significance at the 0.05 probability level.

correlations between the environmental variables at the 5th, 50th, and 95th percentiles of the distribution of the environmental descriptor are shown in Table 8. In the case of CI, genetic correlations were close to unity when herd size was considered as an environmental descriptor but decreased to as low as 0.58 between the 5th and 95th percentiles when AHLMY was used as an environmental descriptor. To further test whether this low correlation was an artifact of the RR model, 305-d milk yield and CI (total data of approximately 51,000 cows) were analyzed in low (below 4,500 kg, which consisted of approximately the bottom 5% of the cows) and high (above 8,000 kg, which consisted of approximately the top 5% of the cows) AHLMY in a 4-trait model (Table 9). This analysis showed that the low genetic correlation between CI in low and high AHLMY was not an artifact of the RR model (0.74 ± 0.29). At this stage, because of the low heritability of CI and the difficulty of estimating accurate genetic correlations, the evidence for $G \times E$ is inconclusive.

In the case of survival, the difference in heritability and genetic correlation value between low (5th percentile) and high AHLMY (95th percentile) shown in Table 8 was not confirmed by bivariate analyses of low- and high-producing herds. When survival data of cows in low (below 4,800) and high AHLMY (above 7,800) were analyzed by using a bivariate model, the heritability of survival was 0.023 in low- and 0.014 in high-producing herds, and the genetic correlation was 0.81 (compared with 0.31 from the RR model). When herd size was used as an environmental descriptor, only the model with the intercept component converged (Table 8).

In the case of CFS, heritabilities decreased with increasing herd size and AHLMY. Genetic correlations, particularly between the 5th and 95th percentiles, regardless of the herd environmental descriptor used, were below 0.6 for CFS. To further explore whether the greater heritabilities at low levels of average milk yield were an artifact of the RR model, 2 data sets were formed and CFS was analyzed in each data set as a different trait in a bivariate sire model. The first data set included CFS records when the AHLMY was below 6,165 kg and the second included CFS records when it was above 6,165 kg. The heritability of CFS with AHLMY below 6,165 kg was 0.09, and with AHLMY above 6,165 kg it was only 0.03. This difference is due to the large difference in the estimated genetic variance without a marked change in the residual variance. The genetic correlation between the 2 CFS measures (below or above 6,164 kg) was reasonably high at 0.82. The mean CFS and AHLMY were 84 d and 5,317 kg in the first data set and 86 d and 7,093 kg in the second data set, respectively. The genetic correlation between 305-d milk yield and CFS was zero in the first data set (i.e.,

Table 8. Mean environmental descriptor, heritabilities (h^2), phenotypic variance (σ^2), and mean value of the trait at the 5th, 50th, and 95th percentiles of environmental descriptors and genetic correlations for fertility traits

Trait or environmental descriptor	5%					50%					95%					$r_{g, 50}$ and 95%
	$\bar{X}^1$	h^2	σ^2	$\bar{Y}^2$	$\bar{X}^1$	h^2	σ^2	$\bar{Y}^2$	$\bar{X}^1$	h^2	σ^2	$\bar{Y}^2$	$\bar{X}^1$	h^2	σ^2	$r_{g, 5}$ and 95%
Calving interval																
Herd size, n	81	0.04	5,187	410	193	0.03	4,918	407	500	0.03	4,841	404	500	0.03	4,841	0.99
AHLMY, ³ kg	4,429	0.03	5,187	411	6,184	0.03	5,187	405	8,259	0.03	5,187	415	8,259	0.03	5,187	0.89
Survival																
Herd size	81	0.02	1,162	83	193	0.02	1,162	85	500	0.02	1,162	87	500	0.02	1,162	1.0 ³
AHLMY, ³ kg	4,384	0.06	1,165	81	6,180	0.02	1,153	85	8,264	0.01	1,149	88	8,264	0.01	1,149	0.54
Calving to first service interval																
Herd size	96	0.04	754	87	231	0.05	446	81	606	0.01	239	77	606	0.01	239	0.62
AHLMY, ³ kg	4,527	0.10	406	80	6,164	0.05	484	79	8,236	0.04	529	87	8,236	0.04	529	0.76
First service nonreturn rate																
Herd size	96	0.01	2,091	56	237	0.01	2,086	54	609	0.01	2,082	52	609	0.01	2,082	0.81
AHLMY, ³ kg	4,429	0.01	2,091	55	6,184	0.01	2,089	54	8,259	0.01	2,088	54	8,259	0.01	2,088	0.92
Temperature-humidity index	58	0.01	2,085	56	76	0.01	2,087	54	92	0.02	2,091	53	92	0.02	2,091	0.97

¹Mean value of the environmental descriptor at 5th, 50th and 95th percentile.

²Mean value of the trait at the bottom 5% or top 5% of the cows and middle 50%.

³Average herd lactation milk yield.

⁴Only the model with the linear component fitted converged.

Figure 4. Effect of temperature-humidity index (THI) on first service nonreturn rate (%) of cows estimated by fitting cubic spline to THI following Verbyla et al. (1999).

low AHLMY) and 0.38 in the second data set. The corresponding environmental correlations were 0.17 and 0.12 in the first and second data sets, respectively.

The effect of THI on the day of mating on NRR in Figure 4 shows a decrease in NRR with an increase in THI. Genetic correlations between the 5th and 95th percentiles of distributions were approximately 0.8 regardless of the environmental descriptor (Table 8) for NRR.

DISCUSSION

Genotype × Calving System or Region Interaction

Estimates of a genotype × calving system interaction for yield traits observed in the current study are in agreement with previous studies elsewhere (Boettcher et al., 2003; Kearney et al., 2004a) that have reported high heterogeneity of variance and heritability (i.e., G × E attributable to scale). The lowest genetic correlation,

of 0.97, between split and year-round calving herds for protein yield observed in the current study was greater than the lowest genetic correlations between pasture-based grazing and conventional systems in Canada (Boettcher et al., 2003) and the United States (Weigel et al., 1999; Kearney et al., 2004a). For fertility traits such as CFS, pregnancy, and NRR, the genetic correlations for a trait expressed in different calving systems are similar to those observed by Boettcher et al. (2003) and Kearney et al. (2004b).

Compared with yield traits, the genotype × calving system is likely to have more influence on fertility traits because the herd management system directly affects the traits that are measured. For example, for farmers who practice seasonal calving, fertility is very important as compared with farmers who manage year-round calving herds. In the current data, the fewer numbers of records on CFS, pregnancy, and NRR from year-round calving herds as compared with split calving herds perhaps reflects the difference in management emphasis

Table 9. Heritabilities (on diagonal), genetic (below diagonal) and residual correlation (above diagonal) for calving interval and 305-d milk yield in herds with bottom 5% and top 5% of average herd lactation milk yield (AHLMY)

Trait	Production level	Calving interval		305-d milk yield	
		Low	High	Low	High
CI	Low	0.02 ± 0.01 (5,808) ¹	0 ²	0.11 ± 0.01	0 ¹
	High	0.74 ± 0.29	0.03 ± 0.01 (5,052) ¹	0 ²	0.16 ± 0.01
Milk yield	Low	0.3 ± 0.19	0.47 ± 0.16	0.19 ± 0.03 (376,800) ¹	0 ²
	High	0.49 ± 0.20	0.58 ± 0.12	0.87 ± 0.06	0.29 ± 0.03 (106,300) ¹

¹Phenotypic variance estimates are in parentheses.
²Residual correlation not defined.

between the systems (Table 1). Despite this obvious difference, we were not able to detect a large $G \times E$ for fertility traits. This may be because $G \times E$ for traits with low heritability are difficult to detect compared with traits with high heritability (Calus et al., 2004). The large heterogeneity of variance between calving systems (Table 5) and regions (Table 7) for CFS may be related to the way mating data are recorded in each situation. In seasonal calving herds and in regions 2 and 3, the AI mating season is shorter and cows that do not mate during this period are naturally mated so are not recorded. On the other extreme, in year-round calving herds, which are mainly found in region 1, CFS was the longest because some farmers attempt to record all matings.

The results for a $G \times E$ between calving systems or regions in the current study should be reasonably reliable for most traits such as CI, survival, and milk yield traits, for which more than 80% of the records analyzed were from bulls with progeny in the 3 calving systems or 3 regions. However, for some fertility traits, such as pregnancy rate, CFS, and NRR, the number of records, particularly from year-round calving herds, was small, so the results should be interpreted with caution. The lower genetic correlation estimates for CI and survival between split and year-round calving herds compared with that between seasonal and year-round calving herds (Table 5) were unexpected. This may be due to the small data set of split calving herds and also perhaps because of the diverse nature of the herds (Table 3) that are categorized into this group. Table 3 shows that split calving herds are almost evenly distributed in the 3 different regions, whereas the majority of year-round herds are from region 1 and seasonal calving herds are from regions 2 and 3. Furthermore, Table 1 shows that the standard deviations of CI and 305-d milk yield are the greatest for split calving herds.

A recent survey of Australian dairy farmers showed that farmers in Victoria were the least satisfied with the current genetic evaluation system because of $G \times E$ (Paine and Alexander, 2007). The current results show that the genetic correlations between regions 1 (New South Wales, Queensland, West and South Australia) and 3 (Gippsland and Tasmania) were significantly different from unity for both milk and fat yield and between regions 2 (North and West Victoria) and 3 for fat yield (Table 7). For the other traits, the major reason for the observed genotype $\times$ region interaction was the scaling effect, rather than actual reranking. For milk yield traits, genetic correlation estimates between regions in Australia were similar to those estimated between states in the United States (Carabaño et al., 1990). Genetic correlations of between 0.9 and 0.95 were estimated between milk yield traits recorded in West

and East Germany (König et al., 2005). Estimates of a genotype $\times$ region interaction for fertility traits are not available in the literature.

Protein percentage was analyzed to examine whether there was an important $G \times E$ and to assess the possibility of using this information to identify bulls that could produce progeny with a relatively high protein percentage for use in region 1 (mainly West Australia and Queensland). This is important because some herds in these states provide milk that is unacceptable for processing (below 3% protein) during the summer months (White et al., 2004) because of its low protein concentration. In agreement with White et al. (2004), the mean protein percentage in region 1, where West Australia and Queensland were included, was slightly lower than in regions 2 and 3 (Table 2). Furthermore, the mean protein percentage in herds from West Australia and Queensland was lower (3.07%) than the average for all cows in region 1 (3.13%). Despite this, the very high genetic correlations between regions suggest that there was little $G \times E$ (Table 7) and that farmers in these regions might benefit from using bulls with a high protein percentage. However, it might be useful to examine this in the future to see whether there were bulls that sired cows with high protein percentages in environments in which herd-test-day protein percentages were low. If available, these sorts of bulls could be recommended to farmers where this problem exists. At this stage, identifying and using bulls that sire daughters with high protein percentages in herds with low protein percentages may help to alleviate this problem.

Genotype $\times$ Continuous Environmental Descriptors Interaction

The observed differences in heritability of fertility traits over the environmental trajectories were similar to those observed by Kolmodin et al. (2002) and Calus (2006). For fertility traits, the decrease in heritability with an increase in herd size may be related to the difficulty that large herds in pasture-based grazing systems may have in correctly detecting estrous (García and Fulkerson, 2005) and recording mating dates or results. Large herds are also more likely to use synchronization of estrous and timed AI compared with small herds. If this is true, records from large herds were less reliable (did not reflect the ability of a cow to show heat after calving) than those from small herds, and this could result in different heritabilities. The decline in heritability with an increase in AHLMY may also suggest that farmers with low-producing herds are keen to mate cows that show estrous. On the other hand, farmers that manage high-producing herds may consider the level of

milk yield before deciding to inseminate a cow. This is supported by the observed difference in genetic correlation between CFS and milk yield in low-producing (0.0) vs. high-producing (0.38) herds. This association may make mating data from high AHLMY herds less reliable than those from low AHLMY herds, as observed in the current heritabilities. Deliberate delay of mating, which may also result in low heritability, is likely to be more common in year-round calving herds than in split calving herds. In the case of seasonal calving herds, the attempt to have a tighter calving period may involve frequent use of synchronization of estrous and timed AI, which may undermine the value of traits such as CFS. Goodling et al. (2005) reported that length of the CFS and its heritabilities are influenced by synchronizations.

The slight increase in heritability of NRR with an increase in THI is in agreement with Oseni et al. (2004), who observed high heritability for days open when heat stress levels were high. The decrease in NRR per unit increase in THI of 0.2% observed in the current study is similar to that reported by Ravagnolo and Misztal (2002) in the United States.

General Discussion

In the current study, when calving systems or regions were used as the environment, the estimated genetic correlations were above 0.89 for all milk yield traits. Hayes et al. (2003) estimated the $G \times E$ between the 5th and 95th percentiles to be as low as 0.7 for test-day fat yield when average herd test-day protein yield was used as the environmental descriptor. This may imply that average herd test-day protein yield is a better environmental variable to describe a unique environmental situation than is calving system or region. In the current study, when 305-d milk yield was analyzed by using AHLMY as environmental variable, the genetic correlation between the 5th and 95th percentiles was 0.86 (results not tabulated) and was the same as the result in Table 9 from the 4-trait analysis. This is similar to a genetic correlation of 0.83 for test-day milk yield between the 5th and 95th percentiles of average herd test-day protein yield reported by Hayes et al. (2003) based on Australian data.

Robertson (1959) suggested that the impact of a $G \times E$ is economically important if the genetic correlation of a trait expressed in different environments falls below 0.8. Recently, Mulder et al. (2006) recommended that the genetic correlation should be below 0.61 before separate breeding schemes for environments of equal importance would become better than a single scheme. In this study for most traits, genetic correlations be-

tween calving systems or regions were greater than 0.8, showing little evidence of major sire reranking. When $G \times E$ were tested for continuous environmental descriptors such as herd size and AHLMY, genetic correlations between extreme groups (top or bottom 5%) of herds, which represent a small fraction of the population, were approximately 0.6 for some fertility traits (NRR, CFS, and pregnancy). Even for the traits with low correlations, the advantages of separate genetic evaluations should be carefully weighed against the disadvantages. Separate genetic evaluations would increase the number of EBV that farmers receive and could possibly introduce more confusion. The majority of the data for genetic evaluation in Australia comes from seasonal calving systems (mainly Victoria), and they can select sires accurately based on current rankings. The other option is to account for $G \times E$ in the current genetic evaluation system, for example, as suggested by Kolmodin et al. (2002). However, this could succeed only if accompanied by an extensive farmer education program.

Selection of sires in Australia is based on an index that includes production, fertility, and functional traits (Australian profit ranking), and even in the absence of a $G \times E$ for individual traits, there can be a $G \times E$ for the economic index (Namkoong, 1985). In addition, fertility may be economically more important, for example, in a seasonal than in a year-round calving system. Furthermore, differences between bulls in breeding value for milk production traits could be less in low-production herds (e.g., seasonal calving herds) and therefore worth less in dollars, whereas the differences in fertility might be the same or even higher in low-production herds, causing a reranking of the bulls for profit. Calus et al. (2005) demonstrated that the relative importance of fertility traits to production traits was influenced by production environments in the Netherlands. Therefore, the consequence of a $G \times E$ for profitability is ultimately more important than its effect on a single component, and this will be a topic for future study.

Kearney et al. (2004a) questioned whether grazing herds, especially in very extensive conditions, can afford to pay as much for the semen of bulls transmitting the greatest yields. Currently in Australia, owners of seasonal or split calving herds recognize the importance of fertility traits in their system (e.g., more recording of fertility data), and the results of this study also suggest that they will benefit more if they select among the top bulls for fertility traits. Farmers could do this by using customized economic selection indices similar to those developed by Bowman et al. (1996).

CONCLUSIONS

For most traits, differences in mean performance, variance, and heritability were observed when cows were recorded in different environments. However, genetic correlations between calving systems or regions for milk yield traits, CI, and survival, where data were adequate, were always greater than 0.8. The lowest genetic correlations, of approximately 0.6, were estimated for some fertility traits such as CFS and NRR, which have low heritability. However, these estimates are likely to be associated with large sampling variance because of the small data set and poor connectedness. At least for milk yield traits, there was no evidence of the presence of $G \times E$ resulting in the reranking of bulls that could be considered economically significant.

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