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Genetic analysis of fertility in the Italian Brown Swiss population using different models and trait definitions

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ABSTRACT

The aim of this study was to estimate genetic parameters for fertility and production traits in the Brown Swiss population reared in the Alps (Bolzano-Bozen province, Italy). Fertility indicators were interval from parturition to first service, interval from first service to conception (iFC), and interval from parturition to conception, either expressed as days and as number of potential 21-d estrus cycles (cPF, cFC, and cPC, respectively); number of inseminations to conception; conception rate at first service; and non-return rate at 56 d post-first service. Production traits were peak milk yield, lactation milk yield, lactation length, average lactation protein percentage, and average lactation fat percentage. Data included 71,556 lactations (parities 1 to 9) from 29,582 cows reared in 1,835 herds. Animals calved from 1999 to 2007 and were progeny of 491 artificial insemination bulls. Gibbs sampling and Metropolis algorithms were implemented to obtain (co)variance components using both univariate and bivariate censored threshold and linear sire models. All of the analyses accounted for parity and year-month of calving as fixed effects, and herd, permanent environmental cow, additive genetic sire, and residual as random effects. Heritability estimates for fertility traits ranged from 0.030 (iFC) to 0.071 (cPC). Strong genetic correlations were estimated between interval from parturition to first service and cPF (0.97), and interval from parturition to conception and cPC (0.96). The estimate of heritability for cFC (0.055) was approximately double compared with iFC (0.030), suggesting that measuring the elapsed time between first service and conception in days or potential cycles is not equivalent; this was also confirmed by the genetic correlation between iFC and cFC, which was strong (0.85), but more distant from unity than the other 2 pairs of fertility traits. Genetic correlations between number of inseminations to conception, conception rate at first service, non-return rate at 56 d post-first service, cPF, cFC, and cPC ranged from 0.07 to 0.82 as absolute value. Fertility was unfavorably correlated with production; estimates ranged from −0.26 (cPC with protein percentage) to 0.76 (cPC with lactation length), confirming the genetic antagonism between reproductive efficiency and milk production. Although heritability for fertility is low, the contemporary inclusion of several reproductive traits in a merit index would help to improve performance of dairy cows.

Key words: censored, dairy cow, fertility, genetic parameter

INTRODUCTION

Female fertility is a complex trait and comprises the ability of the cow to return in heat within an acceptable period after calving, to show heat in a proper manner, and to become pregnant with a limited number of inseminations (Groen et al., 1997). A relevant body of literature links selection for milk yield traits to a general loss of reproductive fitness, health, and longevity (Dematawewa and Berger, 1998; Lucy, 2001; Wall et al., 2003), and the genetic antagonism between yield and fertility has often been indicated as the major factor leading to hampered reproductive performance (Hansen et al., 1983; Oltenacu et al., 1991).

The decline in fertility has supposedly come from an increase of energy utilization from the mammary gland and a subsequent amended hormonal and metabolic profile. This might have an influence on the reproductive organs, leading to low ovulation rates, weak estrus, and decreased success in embryo establishment (Veerkamp et al., 2003). Although losses of reproductive efficiency have been relevant in the major dairy populations (Hare et al., 2006), several authors reported that the genetic improvement of fertility is viable (Andersen-Ranberg et al., 2005; Holtsmark et al., 2008; Heringstad and Larsgard, 2010). Fertility traits are usually characterized by low heritability and they are often more influenced by non-additive than additive genetic effects (Fuerst and Sölkner, 1994).

Predicted breeding values for reproductive performance often rely on calving interval (i.e., the time

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between 2 subsequent calvings). This trait is easier to record and is much less affected by data quality than other measures of fertility such as number of inseminations to conception (**INS**) and conception rate at first service (**CFS**). However, it is not available for cows culled before subsequent calving, leading to overestimation of reproductive efficiency. Also, calving interval is a late measure of fertility, as it is available approximately 1 yr after the beginning of estrus activity, with a delayed publication of breeding values for progeny-tested bulls. Because of these limitations, efforts are needed to look for related traits which could be useful as early indicators of reproductive efficiency (Berry et al., 2003; Dal Zotto et al., 2007; König et al., 2008).

The use of direct measures of fertility other than calving interval could lead to more timely results in breeding programs, provided that phenotypic data are reliable and that they are modeled correctly. Nonreturn rate at 56 d post-first service (**NR56**) is one of the most used traits as it allows for a fast evaluation of reproduction performance, without the need of waiting for the subsequent calving; it is commonly taken into account both to infer genetic parameters for fertility in dairy cows (Jamrozik et al., 2005; König et al., 2008) and to routinely evaluate bulls on a national (Andersen-Ranberg et al., 2005; Gredler et al., 2007; Miglior, 2007) and an international basis (Biffani and Canavesi, 2007). An important drawback of NR56 is that it considers successful those inseminations that are not followed by a subsequent breeding within 56 d, without validation through subsequent calving.

One of the major limitations with fertility is that it cannot be fully represented by a single measure, but rather by a complex of measures, including non-normal and categorical traits. Conception rate at first service and NR56 are dichotomous variables, and INS is a count and highly skewed trait. The intervals between parturition to first service (**iPF**), first service to conception (**iFC**), and parturition to conception (**iPC**) are conceptually based on a categorical number of estrus cycles and are again characterized by highly skewed distribution. Furthermore, not all estrus cycles lead to an insemination because of the voluntary waiting period, non-observed heat, and health disorders; not all inseminations result in a conception because of infertility issues; and not all conceptions lead to a subsequent calving because of abortions, death of the cow or, simply, lack of information. All of these aspects reinforce the complexity of defining reproduction efficiency. Finally, the beginning and end of each estrus cycle are not regularly recorded at the population level and insemination and parturition information is sometimes lacking as well (censored data). Modeling the intervals in terms of number of potential 21-d cycles and use of censored threshold models has been recently proposed to overcome some of these limitations (Chang et al., 2007).

In Bolzano-Bozen province (northeastern Italian Alps), an efficient AI recording scheme is currently running and the majority of inseminations are carried out by veterinarians. The Brown Swiss is the most important breed of this province and accounts for approximately 41% of cows involved in monthly test-day milk recording. On a national basis, the province represents about 25% of the whole Brown Swiss population enrolled in the milk recording scheme. Italian Brown Swiss has been characterized for several important production aspects such as milk coagulation properties (De Marchi et al., 2007) and yield and quality of cheese (De Marchi et al., 2008). However, information on genetic aspects of female fertility within the population is scarce and limited to calving interval (Dal Zotto et al., 2007) or to success rate (Rizzi et al., 2009). Outside Italy, Brown Swiss breed has been studied for fertility in Germany (Distl, 1991), Austria (Fuerst and Sölkner, 1994), and Mexico (Estrada-León et al., 2008).

The aim of this study was to infer (co)variance components and related parameters for several fertility traits using censored linear and threshold models, and to estimate genetic correlations between fertility and production in the Italian Brown Swiss population.

MATERIALS AND METHODS

Data Collection and Editing Procedure

Insemination and production records on Brown Swiss cows were obtained from the Breeders Association of Bolzano-Bozen province (Italy). Data included 71,556 lactations from 29,582 cows (parities 1 to 9) reared in 1,835 herds; animals calved from 1999 to 2007 and were progeny of 491 AI bulls. To limit the potential effect of selection bias due to culling for both production and fertility issues, sequential edits were applied and second and later lactations were only retained if a first-lactation record was available. Following this approach, distribution of data across parities was as follows: 29,582 records on first lactation, 19,140 records on second lactation, 11,360 records on third lactation, and 11,474 records on fourth and later lactations. Production traits considered were peak milk yield (**pMY**, kg), lactation milk yield (**lMY**, kg), lactation length (**LL**, d), average lactation protein percentage (**PP**, %), and average lactation fat percentage (**FP**, %). Fertility traits included both success and interval indicators. Success traits were INS, CFS, and NR56. The first one was coded as an ordinal categorical variable according to the number of services needed to achieve pregnancy,

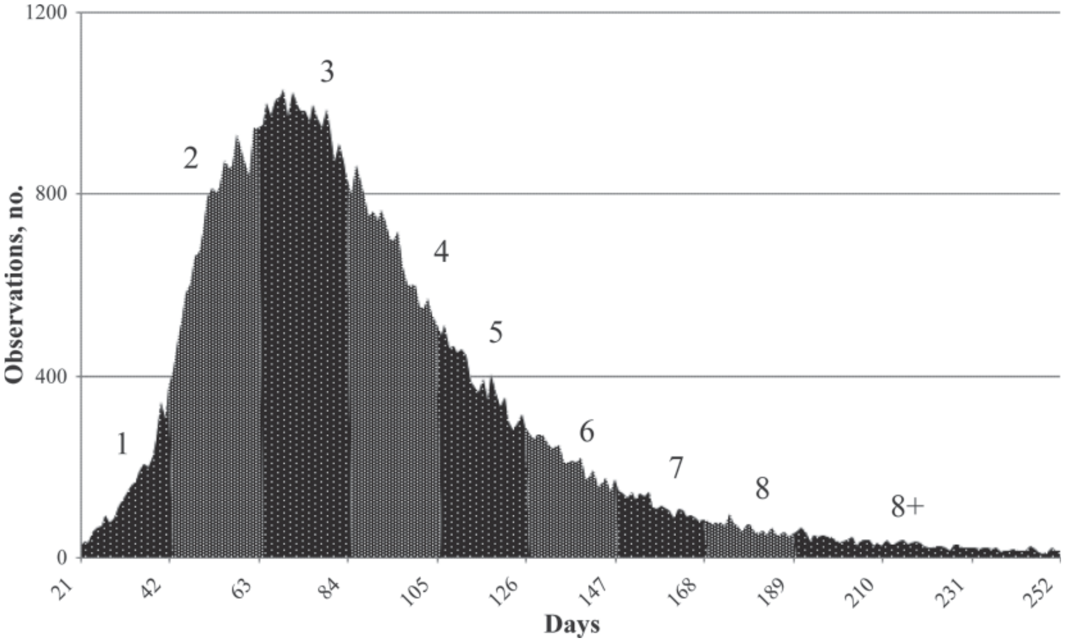

Figure 1. Distribution of records across days from 21 d after parturition to first service. Different shadings are intervals of 21 d.

and inseminations occurring within 6 d were considered as a single service. The variable consisted of 5 classes, the last being an open class including lactations with more than 4 services. Conception rate at first service and NR56 were coded as dichotomous variables according to the achievement of pregnancy at first service for CFS, or the occurrence of a second breeding within 56 d after first service (0) or not (1) for NR56. Records for INS were considered censored if subsequent calving was not recorded or more than 4 services occurred. Traits iPF, iFC, and iPC were edited as follows: between 21 and 252 d for iPF (i.e., eleven 21-d cycles), between 0 and 336 d for iFC (i.e., fifteen 21-d cycles), and between 21 and 336 d for iPC (i.e., sixteen 21-d cycles); iFC and iPC were considered censored if a subsequent calving was not recorded. In addition, the number of potential cycles from parturition to first service (**cPF**), from first service to conception (**cFC**), and from parturition to conception (**cPC**) were calculated from iPF, iFC, and iPC, respectively. The 3 categorical variables were represented by 8 longitudinal 21-d classes. For cPF and cPC, the 21-d intervals started from the edited minimum of 21 d after calving, so that the first class grouped records between 21 and 42 d, the second between 43 and 64 d, and so on up to the 8th class. For cFC all records for iFC = 0 (cows pregnant at first service) were grouped in the first class, the second class grouped records for iFC between 7 and 33 d, and the third and subsequent classes grouped records in 21-d classes starting from iPF = 33 d. Records exceeding 8 cycles were clustered into the eighth class and treated as censored, besides the censoring criterion for the respective days-measured trait (missing subsequent calving for iFC and iPC). Figures 1, 2, and 3 depict the distributions and 21-d clustering of iPF and cPF, iFC and cFC, and iPC and cPC, respectively.

Herds with less than 5 observations were discarded, as well as cows that moved to a different herd during the breeding period within a given lactation. Sires were required to have a minimum of 10 observations distributed across at least 3 herds and 3 daughters.

Statistical Analysis

Univariate Censored Linear Model. A mixed censored linear model (Carriquiry et al., 1987; Sorensen et al., 1998; Guo et al., 2001) was used for the analysis of production and days-measured interval traits (i.e., iPF, iFC, and iPC). The model may be written as

$$y_i = x_i^{'}\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s} + e_i,$$

where y_i is the observed (non-censored record) of cow i; $x_i^{'}$, $z_{h,i}^{'}$, $z_{p,i}^{'}$, and $z_{s,i}^{'}$ are incidence vectors related to location vector $\boldsymbol{\beta}$ (parity effect: 4 classes with the last class including parities 4 to 9; year-month of calving effect: 108 classes), herd effect ($\mathbf{h}$), permanent environmental effect of the cow ($\mathbf{p}$), and sire transmitting abilities ($\mathbf{s}$), respectively; and e_i is the residual. Unobserved respons-

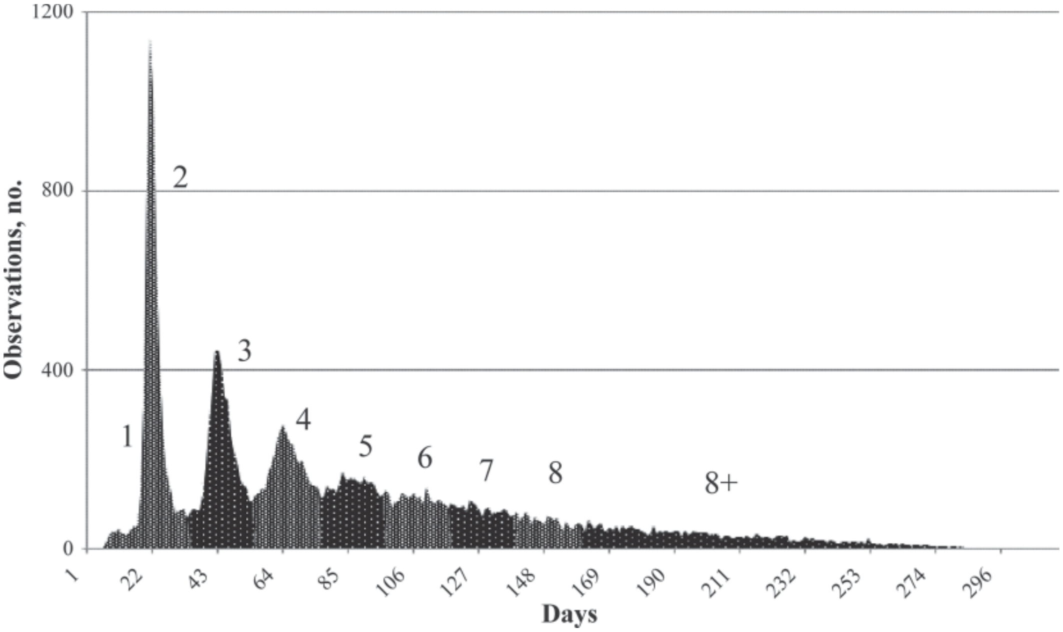

Figure 2. Distribution of records across days from first service to conception. Different shadings are intervals of 21 d; interval 1 (0 d, cows pregnant at first insemination) has been voluntarily omitted due to high frequency (n = 39,732).

es for censored records can be augmented using a truncated normal process as

$$\tilde{y}_c \sim N\left(x_c'\boldsymbol{\beta} + z_{h,c}'\mathbf{h} + z_{p,c}'\mathbf{p} + z_{s,c}'\mathbf{s}, \sigma_c^2\right) I\left(y_c, \infty\right),$$

where y_c is the observed censoring time, such that the augmented values are larger than the censoring point.

Univariate Censored Threshold Model. The threshold model was used for the analysis of cycles-measured traits (i.e., cPF, cFC, and cPC), which were treated as ordinal categorical variables with 8 classes and 7 thresholds, and INS, CFS, and NR56, which were ordinal categorical and binary (0/1) variables as described previously. The threshold model postulates a mixed effect model in the scale of a latent variable, li-

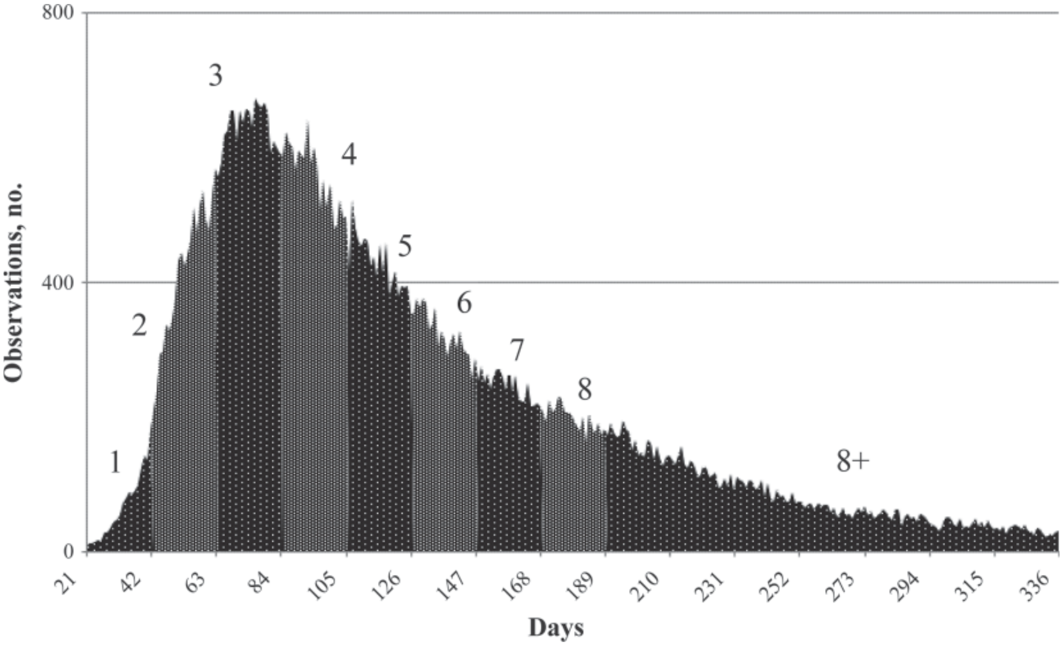

Figure 3. Distribution of records across days from 21 d after parturition to conception. Different shadings are classes of 21 d.

ability (λ), for each observation (Gianola, 1982; Gianola and Foulley, 1983). The observation takes the value j only if λ is greater than or equal to $T_{j\text{-}1}$ and smaller than T_j, where $T_{j\text{-}1}$ and T_j are unknown thresholds. The probability model can be written as

$$\operatorname{Prob}\left(y_i = j \mid \boldsymbol{\beta}, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}\right) = \Phi\left[T_j - \left(x_i\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right] \\ -\Phi\left[T_{j-1} - \left(x_i\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right],$$

where $j = 1, 2, \ldots, j$ indexing the category in which the observation belongs; $\Phi(\cdot)$ is the standard cumulative normal distribution function, and $\mathbf{T} = [T_0, T_1, T_2, \ldots, T_j]'$ is the vector of unknown thresholds. The thresholds must satisfy $-\infty = T_0 \le T_1 \le T_2 \le \ldots \le T_j = \infty$. The first threshold T_1 is set to zero, because the parameter cannot be identified in a probit analysis. This concept, as previously reported by Chang et al. (2006), accommodates situations in which records are censored at the last observed point. If an observation is censored at the jth insemination, and its status is not pregnant, then its corresponding liability must be larger than T_j. The probability that the observation is censored at the jth category is

$$\operatorname{Prob}\left(y_i = j, \text{censored} \mid \boldsymbol{\beta}, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}\right) \\ = 1 - \Phi\left[T_j - \left(x_i^{'}\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right].$$

The joint probability of N non-censored and censored data, given the location effects and the thresholds, is

$$\operatorname{Prob}\left(\mathbf{y} \mid \boldsymbol{\beta}, \mathbf{h}, \mathbf{p}, \mathbf{s}, \mathbf{T}, \boldsymbol{\delta}\right) \\ = \prod_{i=1}^{N} \left\{ \begin{matrix} \Phi\left[\mathrm{T}_{y_i} - \left(x_i^{'}\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right] \\ -\Phi\left[\mathrm{T}_{y_i-1} - \left(x_i^{'}\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right] \end{matrix} \right\}^{1-\delta_i} \\ \left\{1 - \Phi\left[\mathrm{T}_{y_i-1} - \left(x_i^{'}\boldsymbol{\beta} + z_{h,i}^{'}\mathbf{h} + z_{p,i}^{'}\mathbf{p} + z_{s,i}^{'}\mathbf{s}\right)\right]\right\}^{\delta_i},$$

where $\boldsymbol{\delta}$ is the vector of censoring indicators and $\delta_i = 0$ if a record is not censored and 1 otherwise.

Bivariate Censored Threshold-Linear and Threshold-Threshold Model. A Bayesian bivariate model was used to infer genetic relationship between fertility traits and between fertility and productions traits. (Co)variance components were obtained fitting threshold-linear (Foulley et al., 1983), and threshold-threshold models (König et al., 2008). Criteria for censoring were the same as in the univariate approach. Right-censored records were included as unknown parameters in the model, using the methodology described by Guo et al. (2001), which is based on a data augmentation procedure (Tanner and Wong, 1987). Systematic effects were the same as for univariate analyses. Flat priors were used for systematic effects and dispersion parameters. Prior distributions for the additive genetic, permanent environmental cow and herd effects were normal densities. In a Bayesian setting, we assumed

$$\begin{bmatrix}\mathbf{s}_1 \\ \mathbf{s}_2\end{bmatrix} \sim N\left(0, \mathbf{G} \otimes \mathbf{A}\right),$$

where $\mathbf{G}\begin{bmatrix}\sigma_{s1}^2 & \sigma_{s12} \\ \sigma_{s21} & \sigma_{s2}^2\end{bmatrix}$ is a 2 × 2 sire transmitting abilities (co)variance matrix, and $\mathbf{A}$ is the numerator relationship matrix between sires. Likewise, permanent environmental cow and herd effects were assumed to follow a multivariate normal distribution:

$$\begin{bmatrix}\mathbf{p}_1 \\ \mathbf{p}_2\end{bmatrix} \sim N\left(0, \mathbf{P} \otimes \mathbf{I}\right)$$

$$\begin{bmatrix}\mathbf{h}_1 \\ \mathbf{h}_2\end{bmatrix} \sim N\left(0, \mathbf{H} \otimes \mathbf{I}\right),$$

where $\mathbf{P}\begin{bmatrix}\sigma_{p1}^2 & \sigma_{p12} \\ \sigma_{p21} & \sigma_{p2}^2\end{bmatrix}$ is a 2 × 2 permanent environmental (co)variance matrix and $\mathbf{H}\begin{bmatrix}\sigma_{h1}^2 & \sigma_{h12} \\ \sigma_{h21} & \sigma_{h2}^2\end{bmatrix}$ is a 2 × 2 (co)variance matrix between herd effects for the 2 traits.

Residuals for linear traits were assumed correlated and normally distributed: $\boldsymbol{e} \sim N(0, \mathbf{R_0} \otimes \mathbf{I})$, with $\mathbf{R}_0$ being the residual (co)variance matrix:

$$\mathbf{R}_0 = \begin{bmatrix}\sigma_{e1}^2 & \sigma_{e12} \\ \sigma_{e21} & \sigma_{e2}^2\end{bmatrix},$$

where σ_{e1}^2 and σ_{e2}^2 are the variances of trait 1 and 2, respectively, and σ_{e12} (or σ_{e21}) is the covariance between the traits. Residual variances were forced to 1 in case of threshold analysis, so that for threshold-linear models the matrix was

$$\mathbf{R}_0 = \begin{bmatrix}1 & \sigma_{e12} \\ \sigma_{e21} & \sigma_{e2}^2\end{bmatrix}.$$

Finally, for threshold-threshold analysis the residual matrix was

$$\mathbf{R}_0 = \begin{bmatrix}1 & \sigma_{e12} \\ \sigma_{e21} & 1\end{bmatrix}.$$

Gibbs Sampler. Gibbs sampling and Metropolis algorithm were implemented for Gaussian and categorical variables, respectively. Such algorithms were extensively detailed in Chang et al. (2006) for censored linear, censored threshold, and bivariate censored threshold-linear models, and in König et al. (2008) for threshold-threshold model. All analyses were performed using software previously developed for similar analyses (Chang et al., 2006). A single Gibbs chain of 250,000 samples was obtained for univariate models, whereas for bivariate models 550,000 iterations were run, discarding the first 50,000 samples as burn-in. The effective length of the burn-in and the chain size were chosen on the basis of the methods of Raftery and Lewis (1992) and Geyer (1992), respectively. Sample values were saved every 20 iterations for the univariate model and 50 iterations for bivariate models. The posterior mean was used as a point estimate of (co)variance components and related parameters. Lower and upper bounds of the 95% highest posterior probability density regions for heritabilities and additive genetic correlations were estimated from the Gibbs samples.

Heritability was computed as

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_p^2 + \sigma_h^2 + \sigma_e^2},$$

intra-herd heritability was calculated as

$$h_{IH}^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_p^2 + \sigma_e^2},$$

herd effect was defined as

$$h_{he}^2 = \frac{\sigma_h^2}{\sigma_s^2 + \sigma_p^2 + \sigma_h^2 + \sigma_e^2},$$

permanent environmental cow effect was computed as

$$h_{pe}^2 = \frac{\sigma_p^2}{\sigma_s^2 + \sigma_p^2 + \sigma_h^2 + \sigma_e^2},$$

and genetic correlations were calculated as

$$\rho_g = \frac{\mathrm{cov}_s(x,y)}{\sigma_{s,x}\sigma_{s,y}}.$$

RESULTS AND DISCUSSION

Fertility Traits

Means for fertility traits of Brown Swiss cows (Table 1) were more favorable than values previously reported for Holstein-Friesians (Dematawewa and Berger, 1998; Berry et al., 2003; Wall et al., 2003), but similar to those reported for other breeds (Andersen-Ranberg et al., 2005; Gredler et al., 2007; Holtsmark et al., 2008). Phenotypic means for fertility in Brown Swiss cows from the present study were different from those reported by Estrada-León et al. (2008) on the same breed in the tropics of Mexico; in particular, the iPC in Estrada-León et al. (2008) was much more unfavorable (172.8 d) compared with our study (124.0 d; Table 1), and showed approximately twice the standard deviation of our findings (117.2 vs. 63.9 d). These results suggest that the environment plays an important role in fertility and that the difference between genotype by environment interaction may exist when comparing data from different rearing conditions.

Estimates of variance components and related parameters are shown in Tables 2 and 3, respectively. Fertility traits can be split into 3 groups: the first includes information on the iPF and cPF; the second includes information on insemination events (iFC, cFC, INS, CFS, and NR56); and the third includes information on iPC and cPC. Results will be discussed according to this grouping.

First Group: Parturition to First Service

The iPF averaged 88.2 d with a standard deviation of 37.3 d (Table 1), and the corresponding values of cPF were 3.64 and 1.67. Heritability and intra-herd heritability estimates for iPF and cPF were similar (0.049 and 0.058, and 0.058 and 0.068, respectively; Table 3). These traits showed quite large herd and permanent environmental cow effects (12.1 to 15.0% of the phenotypic variance), probably because of important differences in the voluntary waiting period among different farms (Gallo et al., 2008) and among cows within farms. The genetic (phenotypic) correlations of 0.97 (0.99) between iPF and cPF (Table 4) were close to unity, suggesting that these 2 variables are essentially the same indicator of fertility. The distribution of records across days from parturition to first service is continuous and cyclic patterns are not evident (Figure 1); this is because the interval is the result of a certain number of estrus cycles, dependent on the voluntary waiting period and the estrus detection rate, but also on the post-parturition anestrous period. Estimates of heritability for iPF are higher than those reported by González-Recio et al. (2006) on Spanish Holsteins and by Estrada-León et al. (2008) on Mexican Brown Swiss cows, but lower than values obtained by Gredler et al. (2007) in dual-purpose Austrian Simmental, and by König et al. (2008) on German Holstein cows. No estimates of heritability for cPF are currently available that the authors are aware of.

Table 1. Descriptive statistics of fertility and production traits, and percentage of censored records

Trait[1]	Mean	SD	Minimum	Maximum	Censored records, %
Fertility trait					
iPF, d	88.2	37.3	21	252	0
cPF, no.	3.64	1.67	1	8	2.39
NR56	0.71	0.46	0	1	0
CFS	0.45	0.50	0	1	0
INS, no.	1.74	1.02	1	5	23.4
iFC, d	36.0	55.4	0	314	16.9
cFC,[2] no.	2.56	2.25	1	8	20.2
iPC, d	124.0	63.9	21	336	16.9
cPC, no.	4.91	2.16	1	8	28.5
Production trait					
pMY, kg	28.5	6.13	6	62	0
lMY, kg	7,120	2,052	378	16,461	1.62
LL, d	327	71.1	26	676	1.62
PP, %	3.57	0.24	2.51	4.78	0
FP, %	4.19	0.42	1.94	7.00	0

[1] iPF = interval from parturition to first service; cPF = potential estrus cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC = potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

[2] Cycles are counted considering cFC = 1 for cows pregnant at first service.

Second Group: Insemination Events. The NR56 averaged 0.71 (Table 1) and exhibited the lowest heritability (approximately 0.04; Table 3) among categorical traits, and often the weakest correlations with other measures of fertility (Table 4). Nevertheless, estimates of heritability for NR56 are higher than those reported by Gredler et al. (2007), who calculated a value of 0.011 with linear models, and König et al. (2008), who reported a value of 0.029 from binary threshold models. The mean value for CFS, validated by subsequent calving, was much lower than NR56 (0.45 and 0.71, respectively; Table 1), confirming that the latter trait largely overestimates fertility. Also, heritability and intra-herd heritability for CFS were higher than NR56 (0.055 and 0.058 vs. 0.037 and 0.039, respectively). These 2 traits are calculated through different procedures (the occur-

Table 2. Estimates[1] of sire $\left(\sigma_s^2\right)$, herd $\left(\sigma_{he}^2\right)$, permanent environmental cow $\left(\sigma_{pe}^2\right)$, and residual $\left(\sigma_e^2\right)$ variance components of fertility and production traits

Trait[2]	σ_s^2	σ_{he}^2	σ_{pe}^2	σ_e^2
Fertility trait				
iPF, d	1.746×10^{1}	2.124×10^{2}	1.919×10^{2}	9.919×10^{2}
cPF, no.	2.011×10^{-2}	1.913×10^{-1}	1.670×10^{-1}	1.00
NR56	1.049×10^{-2}	6.112×10^{-2}	5.342×10^{-2}	1.00
CFS	1.560×10^{-2}	5.153×10^{-2}	6.823×10^{-2}	1.00
INS, no.	1.670×10^{-2}	5.146×10^{-2}	8.822×10^{-2}	1.00
iFC, d	2.737×10^{1}	1.286×10^{1}	3.395×10^{1}	3.138×10^{3}
cFC, no.	1.589×10^{-2}	4.868×10^{-2}	9.224×10^{-2}	1.00
iPC, d	7.326×10^{1}	3.033×10^{2}	7.483×10^{2}	3.774×10^{3}
cPC, no.	2.226×10^{-2}	8.081×10^{-2}	1.512×10^{-1}	1.00
Production trait				
pMY, kg	5.286×10^{-1}	9.716	4.095	1.292×10^{1}
lMY, kg	8.402×10^{4}	9.365×10^{5}	8.778×10^{5}	1.652×10^{6}
LL, d	4.779×10^{1}	3.837×10^{2}	5.043×10^{2}	3.427×10^{3}
PP, %	4.680×10^{-3}	1.644×10^{-2}	1.932×10^{-2}	1.846×10^{-2}
FP, %	1.213×10^{-2}	3.200×10^{-2}	5.978×10^{-2}	6.685×10^{-2}

[1] Estimates are the means of the marginal posterior distributions for the variance components.

[2] iPF = interval from parturition to first service; cPF = potential estrus cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC = potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

Table 3. Estimates[1] of heritability (h^2), intra-herd heritability $\left(h_{IH}^2\right)$, herd effect $\left(h_{he}^2\right)$, and permanent environmental cow effect $\left(h_{pe}^2\right)$ of fertility and production traits

Trait[2]	h^2 (HPD95%)	h_{IH}^2 (HPD95%)	h_{he}^2 (HPD95%)	h_{pe}^2 (HPD95%)
Fertility trait				
iPF, d	0.049 (0.035; 0.066)	0.058 (0.041; 0.078)	0.150 (0.139; 0.162)	0.136 (0.127; 0.144)
cPF, no.	0.058 (0.043; 0.077)	0.068 (0.050; 0.089)	0.139 (0.128; 0.150)	0.121 (0.113; 0.130)
NR56	0.037 (0.027; 0.051)	0.039 (0.028; 0.054)	0.054 (0.048; 0.061)	0.047 (0.035; 0.060)
CFS	0.055 (0.040; 0.073)	0.058 (0.042; 0.077)	0.045 (0.040; 0.052)	0.060 (0.048; 0.072)
INS, no.	0.058 (0.043; 0.076)	0.060 (0.045; 0.080)	0.044 (0.039; 0.050)	0.076 (0.065; 0.088)
iFC, d	0.030 (0.020; 0.043)	0.031 (0.021; 0.044)	0.035 (0.031; 0.040)	0.093 (0.083; 0.104)
cFC, no.	0.055 (0.041; 0.072)	0.057 (0.042; 0.075)	0.042 (0.037; 0.048)	0.080 (0.069; 0.091)
iPC, d	0.060 (0.044; 0.080)	0.064 (0.074; 0.085)	0.062 (0.055; 0.069)	0.153 (0.142; 0.163)
cPC, no.	0.071 (0.053; 0.092)	0.076 (0.057; 0.099)	0.064 (0.058; 0.071)	0.120 (0.111; 0.130)
Production trait				
pMY, kg	0.078 (0.061; 0.097)	0.121 (0.095; 0.150)	0.356 (0.340; 0.374)	0.150 (0.143; 0.158)
lMY, kg	0.095 (0.074; 0.118)	0.129 (0.101; 0.160)	0.264 (0.249; 0.279)	0.247 (0.238; 0.256)
LL, d	0.044 (0.031; 0.059)	0.048 (0.034; 0.065)	0.088 (0.080; 0.096)	0.116 (0.106; 0.125)
PP, %	0.318 (0.269; 0.372)	0.441 (0.376; 0.513)	0.279 (0.263; 0.295)	0.328 (0.318; 0.339)
FP, %	0.284 (0.238; 0.334)	0.349 (0.294; 0.410)	0.187 (0.175; 0.201)	0.350 (0.340; 0.360)

[1] Estimates are the means (lower and upper bound of the 95% highest posterior density region, HPD95%) of the marginal posterior distributions for the parameters.

[2] iPF = interval from parturition to first service; cPF = potential cycles from 21 d after parturition to first service; NR56 = non-return rate at 56 d post-first service; CFS = conception rate at first service; INS = number of inseminations to conception; iFC = interval from first service to conception; cFC = potential estrus cycles from first service to conception; iPC = interval from parturition to conception; cPC = potential estrus cycles from 21 d after parturition to conception; pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage.

rence of a second insemination within 56 d for NR56, and the subsequent calving for CFS), and results from this study led us to infer that they cannot be considered as indicators of the same fertility trait. The INS averaged 1.74 (Table 1), but it should be noted the high incidence of censored records (23.4%) for this trait. Heritability estimate was 0.058 (Table 3), and phenotypic and genetic correlations with other fertility traits were moderate to strong, with few exceptions (Table 4). In general, NR56, CFS, and INS showed moderate to low and unfavorable genetic correlations with cPF (Table 4). Genetic and phenotypic correlations between INS and CFS were −0.78 and −0.73, respectively; the strong relationship between these traits was expected, as CFS is a clustering of INS (CFS = 1 for INS = 1, CFS = 0 for INS >1). Several studies on Holstein-Friesian and Norwegian Red breeds reported values of heritability for INS between 0.01 and 0.04 when estimated using linear models (Dematawewa and Berger, 1998; Wall et al., 2003; Sun et al., 2010), and around 0.04 when estimated through a threshold model (Chang et al., 2006; González-Recio et al., 2006).

The iFC averaged 36.0 d, with very large variability, and the corresponding cFC was 2.56 (Table 1). Heritability estimates for cFC (0.055; lower and upper bound of the 95% highest posterior density region = 0.041 to 0.072) were notably higher than iFC (0.030; lower and upper bound of the 95% highest posterior density region = 0.020 to 0.043). As expected, genetic and phenotypic correlations between the 2 variables were high (0.85 and 0.87, respectively), but significantly lower than between iPF and cPF (Table 4). Thus, iFC and cFC cannot be considered as the same indicator of fertility. Differences might perhaps be due to data modeling, exacerbated by the skewed distribution of iFC. The pattern for this trait is peculiar: the iFC for about half of the cows is zero (cows pregnant at first insemination) and for remaining cows is clearly cyclic (Figure 2).

Third Group: Parturition to Conception. The iPC is the sum of previously described interval traits,

Table 4. Estimates[1] of genetic (ρ_g) and phenotypic (ρ_p) correlations between fertility traits

Trait[2]	cPF		cFC		cPC		INS	
	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p
iPF	0.97 (0.96; 0.98)	0.99 (0.99; 0.99)	0.46 (0.27; 0.63)	−0.07 (−0.08; −0.06)	0.81 (0.73; 0.87)	0.65 (0.65; 0.66)	0.30 (0.09; 0.49)	−0.10 (−0.12; −0.09)
iFC	0.46 (0.26; 0.63)	−0.07 (−0.80; −0.06)	0.85 (0.77; 0.90)	0.87 (0.86; 0.87)	0.83 (0.75; 0.89)	0.79 (0.79; 0.79)	0.67 (0.53; 0.78)	0.85 (0.85; 0.85)
iPC	0.75 (0.65; 0.83)	0.48 (0.47; 0.49)	0.78 (0.69; 0.86)	0.78 (0.78; 0.79)	0.96 (0.94; 0.97)	0.95 (0.94; 0.95)	0.76 (0.66; 0.83)	0.75 (0.74; 0.75)
cPF			0.38 (0.18; 0.54)	−0.07 (−0.08; −0.06)	0.74 (0.65; 0.82)	0.64 (0.63; 0.65)		
cFC					0.76 (0.66; 0.83)	0.75 (0.74; 0.75)		
INS	0.24 (0.03; 0.43)	−0.10 (−0.11; −0.09)	0.82 (0.74; 0.88)	0.78 (0.78; 0.79)	0.66 (0.53; 0.76)	0.68 (0.67; 0.68)		
CFS	−0.33 (−0.51; −0.13)	0.04 (0.03; 0.05)	−0.77 (−0.85; −0.67)	−0.68 (−0.69; −0.67)	−0.64 (−0.75; −0.61)	−0.61 (−0.62; −0.61)	−0.78 (−0.85; −0.68)	−0.73 (−0.74; −0.73)
NR56	0.20 (−0.03; 0.41)	0.13 (0.12; 0.14)	−0.37 (−0.56; −0.16)	−0.48 (−0.49; −0.48)	−0.07 (−0.29; 0.16)	−0.32 (−0.33; −0.31)	−0.46 (−0.63; −0.26)	−0.57 (−0.58; −0.56)

[1] Estimates are the means (lower and upper bound of the 95% highest posterior density region, HPD95%) of the marginal posterior distributions for the correlation.

[2] iPF = interval from parturition to first service; iFC = interval from first service to conception; iPC = interval from parturition to conception; cPF = potential estrus cycles from 21 d after parturition to first service; cFC = potential estrus cycles from first service to conception; cPC = potential estrus cycles from 21 d after parturition to conception; INS = number of inseminations to conception; CFS = conception rate at first service; NR56 = non-return rate at 56 d post-first service.

Table 5. Estimates[1] of genetic (ρ_g) and phenotypic (ρ_p) correlations between production and categorical fertility traits[2]

Trait	cPF		cFC		cPC		INS	
	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p	ρ_g	ρ_p
pMY, kg	0.38 (0.21; 0.53)	−0.01 (0.00; 0.00)	0.28 (0.08; 0.46)	0.05 (0.04; 0.07)	0.35 (0.18; 0.51)	0.02 (0.00; 0.03)	0.24 (0.04; 0.42)	0.07 (0.05; 0.08)
lMY, kg	0.56 (0.42; 0.68)	0.22 (0.20; 0.23)	0.39 (0.21; 0.55)	0.35 (0.34; 0.37)	0.56 (0.43; 0.68)	0.43 (0.41; 0.44)	0.34 (0.16; 0.51)	0.35 (0.33; 0.36)
LL, d	0.64 (0.50; 0.75)	0.37 (0.36; 0.38)	0.61 (0.45; 0.74)	0.50 (0.49; 0.51)	0.76 (0.66; 0.84)	0.66 (0.66; 0.67)	0.54 (0.36; 0.69)	0.45 (0.44; 0.46)
PP, %	−0.23 (−0.38; −0.06)	−0.01 (−0.02; 0.01)	−0.18 (−0.36; 0.00)	0.12 (0.10; 0.13)	−0.26 (−0.41; −0.10)	0.07 (0.06; 0.09)	−0.14 (−0.32; 0.05)	0.13 (0.11; 0.14)
FP, %	−0.03 (−0.20; 0.13)	0.02 (0.00; 0.03)	−0.07 (−0.25; 0.12)	0.05 (0.03; 0.06)	−0.06 (−0.22; 0.11)	0.04 (0.03; 0.05)	−0.08 (−0.25; 0.11)	0.04 (0.03; 0.05)

[1] Estimates are the means (lower and upper bound of the 95% highest posterior density region, HPD95%) of the marginal posterior distributions for the correlation.

[2] pMY = peak milk yield; lMY = lactation milk yield; LL = lactation length; PP = average lactation protein percentage; FP = average lactation fat percentage; cPF = potential estrus cycles from 21 d after parturition to first service; cFC = potential estrus cycles from first service to conception; cPC = potential estrus cycles from 21 d after parturition to conception; INS = number of inseminations to conception.

namely iPF and iFC (Figure 3), and averaged 124.0 d with a standard deviation of 63.9 d (Table 1). The heritabilities for iPC (0.060) and cPC (0.071) were similar (Table 3), and genetic (0.96) and phenotypic (0.95) correlations were close to unity (Table 4). Furthermore, management practices seem to have moderate influence on the traits as outlined by the herd effect, whereas permanent environmental cow was quite relevant (Table 3). Both iPC and cPC showed strong relationships with other fertility traits but NR56, with the absolute value of the estimates being between 0.48 to 0.79 for phenotypic, and between 0.64 and 0.83 for genetic correlations (Table 4). Again, this is not surprising, as iPC and cPC are the result of all other fertility measures. The heritability estimate for iPC was higher than that reported by González-Recio et al. (2006) on Spanish Holsteins and by Estrada-León et al. (2008) on Brown Swiss in the tropics. Regarding cycle-measured variables, Chang et al. (2007) reported a heritability of 0.053 for the number of periods needed to achieve pregnancy in Norwegian Reds, slightly lower than our estimate.

Relationship With Production Traits

Means for production traits of Brown Swiss cows (Table 1) resembled those previously reported by Dal Zotto et al. (2007) and Cecchinato et al. (2009) on the same breed, whereas milk yield was lower and milk contents higher than values from Holstein-Friesians (González-Recio et al., 2006; Cassandro et al., 2008). The heritability for lMY (0.095) was lower than estimates from other studies on the same breed, whereas estimates for FP (0.284) and PP (0.318) were comparable to those from previous studies (Santus et al., 1993; Samoré et al., 2010). Management practices have higher influence on production than fertility traits, as shown by herd effect (Table 3), leading to larger differences between heritability and intra-herd heritability. Our results are in agreement with findings from González-Recio et al. (2006) who assessed a value of 0.20 for herd effect on lMY, very similar to our estimate (0.264). Genetic relationships between fertility and production are reported in Table 5; cPF, cFC, cPC, and INS were positively related to pMY, lMY, and LL, with estimates between 0.24 and 0.76, confirming the genetic antagonism between fertility and production. Phenotypic correlations were similarly unfavorable, except for the estimate between cPF and pMY. Finally, phenotypic and genetic correlations between milk quality traits and fertility were low (−0.26 to 0.13; Table 5). Peak milk yield reflects the production potential of the cow at the usual time of insemination, whereas lMY measures the amount of milk produced by the animal during the entire lactation, and it is affected by the possible lactation elongation resulting from low fertility of the cow. Thus, pMY mainly describes the negative effect of production on fertility caused by the shrinkage of metabolites to the mammary gland at the expenses of the reproductive organs (Veerkamp et al., 2003), whereas lMY outlines the effect of fertility on production. González-Recio et al. (2006) reported genetic correlation of 0.16 between INS and lMY, lower than the value from our study, and König et al. (2008) estimated a genetic correlation of 0.14 between days to first service and lMY, much lower than the value between cPF and lMY form our work.

CONCLUSIONS

Despite being low, results showed that exploitable genetic variation for fertility in the Italian Brown Swiss population exists. Heritability estimates were higher for cycle- than day-measured traits, probably due to the different methods used to assess dispersion parameters; in fact, linear models were applied to continuous variables, whereas threshold models were adopted to analyze cycle traits. In the case of the iFC, the use of potential cycles to express the trait was more appropriate than the use of continuous information; in fact, this interval showed a peculiar skewed distribution, which made it more suitable to be analyzed as cycle trait through threshold than linear models. An unfavorable relationship between fertility and production has been found; this explains the loss of fertility occurring in dairy cattle populations undergoing selection for production traits, even if reared in less-intensive farming conditions such as in the Bolzano-Bozen province. (Co) variance components obtained in the present study can be used to predict the genetic merit of sires for several direct measures of fertility and to improve reproductive efficiency of the population via selection. Further research is needed to investigate how fertility traits can be included in a merit index aiming at reversing the deterioration of reproduction efficiency in Brown Swiss breed. The use of genomic information could be also considered in addition to phenotypic data, thus facilitating the dissection of this complex trait and its genetic improvement.

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