Exploring Different Model Structures for the Genetic Evaluation of Dairy Bull Fertility

Francesco TIEZZI 1 (✉)
Mauro PENASA 1
Christian MALTECCA 2
Alessio CECCHINATO 1
Giovanni BITTANTE 1

Summary

The aim of study was to investigate different models for the evaluation of dairy bulls for male fertility. A dataset containing single insemination records performed on Brown Swiss cows and heifers reared in Eastern Italian Alps was used. The outcome variable (successful/ unsuccessful) was analyzed as binary trait. In the first step raw conception rate was computed for each service sire, as the mean of the outcome of all his insemination events. In the second step Bayesian threshold sire models were implemented via Gibbs sampling. Different models increasing in complexity were fitted, in order to obtain variance components and sire solution estimates. Results showed that genetic variance for direct effect(s) on conception rate is low (repeatability=0.014; heritability=0.009-0.073) and raw conception rate is poorly related to solutions from prediction models. If the service sire is a diagonal effect, rank correlations with raw conception rate are about 0.81-0.84, while those decrease to 0.74-0.78 if service sires are related by a relationship matrix, and is null (-0.01-0.06) if is the sire of the service sire to account for the direct genetic effect. Service sire fertility (sire of service sire effect) has been proven to be a different trait to embryo survival (service sire effect) giving rank correlation of 0.11-0.24. In conclusion phenotypic and genetic differences in male fertility among the service sires exist, and should be monitored thought a reliable evaluation system.

Key words

Brown Swiss, bull fertility, threshold model, heritability

1 University of Padova, Department of Animal Science, Viale dell’Università 16, 35020 Legnaro (PD), Italy ✉ e-mail: francesco.tiezzi@unipd.it
2 North Carolina State University, Department of Animal Science, Raleigh 27695, USA

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Aim

Fertility can be defined as "the accomplishment of pregnancy at the desired time" (Pryce et al., 2004), and it can be viewed as a complex of traits related to the cow (female fertility), the service sire (male fertility) and of the potential calf (embryo survival) as reported by Jansen (1986) and Azzam et al. (1988). While female fertility has been widely studied in the last decades (see Lucy, 2001 for a review), male fertility and embryo survival received less attention. These latter can be defined as "the fertilizing ability of the sperm cells and the viability of the embryo" (Azzam et al., 1988). Fertility, as a trait of the potential calf, has been studied in some papers in the past (Hansen, 1979; Azzam, 1985; Jansen, 1986), and more recently by Andersen-Ranberg et al. (2003). Here, if estimating variance components in a sire model context, the service sires effect (SS) accounts for the embryo survival. A sire-MGS relationship matrix should be included. In this case, all paternal effects (i.e. the male fertility as a trait of the service sire) were considered to be negligible (Azzam et al., 1988). Thus, for the purpose of estimating factors affecting male fertility, the sire of the service sire (SSS) should be included in the model as fixed effect (Nadarajah et al., 1988) or as additive genetic effect (Hyppanen and Juga, 1998; Kuhn and Hutchinson, 2008) if fitting a sire model. It often happens that SS effect is considered as a nuisance variable when estimating the female component of fertility. Within this framework service sires can then be considered unrelated (Weller and Ron, 1992; Weigel and Rekaya, 2000; Jamrozik et al., 2005) or the interaction sire*year of semen production might be of interest (Berry et al., 2010). In both cases, service sires are accounting for their direct genetic effect on embryo establishment and environmental effect on semen quality (Rensing et al., 2006). The inclusion of the effects of both SS and SSS as direct genetic and permanent environmental effects has been proposed to disentangle direct genetic and environmental effects (Murray et al., 1983; Hyppanen and Juga, 1998). Different service sire fertility parameters have been proposed in addition to the ones described. Values for repeatability and heritability for the direct effect on fertility have often been found to be below 10%. Jansen (1986) found a 0.024 heritability for the direct effect on conception rate on heifers, which decreased to 0.013-0.015 in later parities, Andersen-Ranberg et al. (2003) found an heritability lower than 0.01 for non-return at 56 day on heifers estimated with different models. Nadarajah et al. (1988) found a 15.8% heritability for conception rate estimated via sire-son regression. Hyppanen and Juga (1998) found 0.001 heritability for fertility as a trait of the service bull, while Jamrozik et al. (2005) found that service sire permanent environmental variance accounted for 0.1% of total variance. Weigel and Rekaya (2000), comparing linear and threshold models found that service sire permanent environmental variance increased significantly with the latter, still accounting for less than 1%. Male fertility has often been monitored within breeding companies, and these evaluations are not always available to farmers. Moreover, the statistical methodology may, in these cases, be sub-optimal, not accounting for confounding effects, such as herd and cow specific factors (Berry et al., 2010). These often rely on simple means of non-return or conception rate of bulls. Anyway, a different approach in threshold modelling for fertility has been recently proposed and demonstrated to be valuable. This, called product threshold model (David et al., 2009) accounts for the non-additive relationship between factors affecting a binary response, and its performance has been shown on several species (David et al., 2011). The aim of this study was therefore to explore the evaluation of dairy bulls for male fertility in the Italian Brown Swiss population, under different model structures.

Material and methods

A dataset containing more than 200,000 single inseminations records performed on Brown Swiss cows and heifers reared in the province of Bolzano (Eastern Italian Alps) between 1999 and 2008 was constructed. These were validated as successful for conception rate (CR) when giving an acceptable pregnancy length of 288±15 days (mean value from Norman et al., 2009). If two inseminations resulted successful within this range of the pregnancy length the latter was considered successful. If pregnancy length was lower than 273 the cow was not validated as pregnant, and every cow having records in a given lactation was required to have a successful insemination on the previous lactation. From the whole dataset we extracted those inseminations performed with registered AI Brown Swiss bulls as service sire. Service sires were required to have at least 100 observations, herds and technicians were required to have at least 20 observations. Furthermore sires of cows with less than 20 observations and cows at less than two observations were deleted. Leniency in the editing of sires of the cows was stemmed due to the fact that female fertility was considered here just a nuisance variable. Levels, for service sires, herds, technicians and sires of cows, were included if showing a mean for CR bounded between 0.1 and 0.9, in order to avoid bias due to the “extreme category problem”. Although interactions between effects were not fitted (e.g. technician*service sire) those levels showing only one corresponding level for the other effect were edited. For example, a technician was requested to operate in more than one farm and in each farm more than a single technician was supposed to work. This was done for all the effects fitted (except cow* sire of cow). After editing, 124,206 single insemination records were available for further analyses. Different threshold sire model models increasing in complexity were run in a Bayesian framework, in order to obtain and compare variance components and sire solution estimates. For this purpose the software TM by Legarra et al. (2008) was used. All models accounted for the “fixed” effects of year-season of insemination (40 levels), class of parity*dim at insemination (age at insemination for heifers, 26 levels); status of the service sire at insemination (progeny testing/proven, two levels), and the random effects of herd (1,400 levels) and technician (86 levels). A sire pedigree file was built, with software PEDIG (Boichard, 2002) tracing back as many generations as possible. Animal permanent and genetic effects were added sequentially:

— Model A

\[
\lambda = X\beta + Z_h h + Z_t t + Z_{ss}ss + e,
\]

\[
ss \sim N(0,SS \otimes I)
\]

— Model B

\[
\lambda = X\beta + Z_h h + Z_t t + Z_{ss}ss + e,
\]

\[
ss \sim N(0,G \otimes A)
\]

acs
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— Model C
\[ \lambda = \mathbf{X}\beta + Z_h \mathbf{h} + Z_c \mathbf{c} + Z_{ss} \mathbf{ss} + Z_{sc} \mathbf{sc} + \mathbf{e}, \]
\[ c | \mathbf{G} \sim N(0, \mathbf{C} \otimes \mathbf{I}) \]

— Model D
\[ \lambda = \mathbf{X}\beta + Z_h \mathbf{h} + Z_c \mathbf{c} + Z_{ss} \mathbf{ss} + Z_{sc} \mathbf{sc} + \mathbf{e}, \]
\[ \mathbf{sc} | \mathbf{G} \sim N(0, \mathbf{G} \otimes \mathbf{A}) \]

— Model E
\[ \lambda = \mathbf{X}\beta + Z_h \mathbf{h} + Z_c \mathbf{c} + Z_{sss} \mathbf{sss} + Z_{sc} \mathbf{sc} + \mathbf{e}, \]
\[ \mathbf{sss} | \mathbf{G} \sim N(0, \mathbf{G} \otimes \mathbf{A}) \]

— Model F
\[ \lambda = \mathbf{X}\beta + Z_h \mathbf{h} + Z_c \mathbf{c} + Z_{sss} \mathbf{sss} + Z_{ss} \mathbf{ss} + \mathbf{e}, \]
\[ \mathbf{ss} | \mathbf{G} \sim N(0, \mathbf{G} \otimes \mathbf{A}) \]

Where \( \lambda \) is the unobserved liability, assumed continuous and normally distributed, \( \beta \) is the vector of fixed effect, \( \mathbf{h} \) is the vector of herd effects, \( \mathbf{c} \) is the vector of technician effect, \( \mathbf{ss} \) is the vector of service sire effect, \( \mathbf{sc} \) is the vector of cow effect, \( \mathbf{e} \) is the vector of residuals. In model A service sires are assumed as uncorrelated environmental effect, in model B the sire-MG matrix \( \mathbf{I} \), while in model C the sire-MG genetic relationship matrix \( \mathbf{A} \) is included, thus estimating the sire variance for the trait. Model D is similar model B with the inclusion of environmental effect, in order to account for a non-random mating of bulls to cows. In model D the sire of the cow is added as genetic effect for the maternal line, estimating direct-maternal covariances with this model. In model E the service sire genetic effect is substituted with the sire of service sire genetic effect. Model F is similar to the previous but accounting for the environmental effect of service sire as well; in order to disentangle the direct effect in conception between genetic and environmental variance. Solution for the sires levels were obtained solving the BLUP equation with the variance components previously estimated via Gibbs sampling, and Spearman rank correlations were computed. Raw Conception Rate (RCR) was computed for each service sire, as the mean of the outcome of all his insemination events. In the first step correlations were computed among the solutions from models A-D and the RCR for the service sires with observation. Then sires being both service sires and sires of service sires were extracted, and rank correlations between RCR and the solutions from every model were computed.

### Results and discussion
Mean CR was 0.47, while bull RCR averaged 0.46, ranging between 0.10 and 0.60. Variance components and number of levels for each effect are reported in Table 1, service sire repeatabilities and heritabilities are reported in Table 2.

Technician variance was the lowest for most of the models, accounting for less than 1% of total variance. Herd variance was higher but still low, being approximately 2% of total variance. Both technician and herd variances didn’t vary significantly across models. In model A service sires environmental variance was low (0.015) giving a repeatability of 0.014, and it was slightly higher in model B when the relationship matrix was added. In model C and D service sire genetic variance didn’t vary, and for models B-D a heritability of 7% was obtained. Cow environmental variance was estimated at 0.0670 in model C, explaining ~6% of total variance. Similarly an estimated cow environmental variance of 0.0585 was obtained with model D, when the genetic and environmental effects were considered.

### Table 1. Number of levels and posterior means of variance components estimates for Conception at Insemination with the six different models

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Model A</th>
<th>Model B</th>
<th>Model C</th>
<th>Model D</th>
<th>Model E</th>
<th>Model F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serv sire gen var</td>
<td>306</td>
<td>0.0197</td>
<td>0.0205</td>
<td>0.0210</td>
<td>0.0116</td>
<td>0.0024</td>
<td></td>
</tr>
<tr>
<td>Sire of serv sire g.v.</td>
<td>98</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serv sire env var</td>
<td>306</td>
<td>0.0150</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sire of cow gen var</td>
<td>513</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cow env var</td>
<td>28,873</td>
<td>0.0670</td>
<td>0.0585</td>
<td>0.0585</td>
<td>0.0587</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herd variance</td>
<td>1,400</td>
<td>0.0229</td>
<td>0.0229</td>
<td>0.0219</td>
<td>0.0212</td>
<td>0.0209</td>
<td>0.0212</td>
</tr>
<tr>
<td>Technician variance</td>
<td>86</td>
<td>0.0090</td>
<td>0.0090</td>
<td>0.0096</td>
<td>0.0097</td>
<td>0.0098</td>
<td>0.0097</td>
</tr>
<tr>
<td>Residual variance</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total variance</td>
<td>1.0469</td>
<td>1.0516</td>
<td>1.119</td>
<td>1.1208</td>
<td>1.1116</td>
<td>1.1171</td>
<td></td>
</tr>
</tbody>
</table>

### Table 2. Heritabilities on the diagonal, rank correlation between the solutions of the service sires having records (n=306) above the diagonal, and between the solutions of the sires being both service sires and sires of service sires (n=48) below the diagonal

<table>
<thead>
<tr>
<th></th>
<th>Raw CR</th>
<th>Model A</th>
<th>Model B</th>
<th>Model C</th>
<th>Model D</th>
<th>Model E</th>
<th>Model F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raw CR</td>
<td>0.84</td>
<td>0.77</td>
<td>0.76</td>
<td>0.74</td>
<td></td>
<td>0.81(1)</td>
<td>0.98(2)</td>
</tr>
<tr>
<td>Model A</td>
<td>0.75</td>
<td>0.014(1)</td>
<td>0.98</td>
<td>0.97</td>
<td>0.97</td>
<td></td>
<td>0.95(2)</td>
</tr>
<tr>
<td>Model B</td>
<td>0.66</td>
<td>0.98</td>
<td>0.075</td>
<td>0.99</td>
<td>0.99</td>
<td></td>
<td>0.95(2)</td>
</tr>
<tr>
<td>Model C</td>
<td>0.67</td>
<td>0.97</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td></td>
<td>0.95(2)</td>
</tr>
<tr>
<td>Model D</td>
<td>0.66</td>
<td>0.98</td>
<td>0.99</td>
<td>0.99</td>
<td>0.075</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model E</td>
<td>0.06</td>
<td>0.11</td>
<td>0.19</td>
<td>0.18</td>
<td>0.18</td>
<td>0.042</td>
<td></td>
</tr>
<tr>
<td>Model F</td>
<td>-0.01</td>
<td>0.14</td>
<td>0.24</td>
<td>0.23</td>
<td>0.23</td>
<td>0.78</td>
<td>0.009</td>
</tr>
</tbody>
</table>

1 Service sire repeatability; 2 For model F solutions for the service sire as permanent environmental effect are considered.
netic effect of the sire of cow was added. This effect counted for less than 1% of total variance; with most of the maternal component falling in the cow environmental effect. In model E and F the animal genetic effect was substituted with the sire of the service sire. In model E, sire of service sire additive genetic variance was estimated at 0.0116, with an heritability of 4.2%, lower than the additive genetic variance estimated in models B, C, D. The same variance was reduced to 0.0024 when the service sire was added as environmental effect, which accounted for the 1.3% of total variance, and the variance adsorbed by this effect was therefore equal to that one estimated in model A. Variance components for the maternal effect were not affected when shifting to the two latter models. Rank correlations computed between RCR and solutions for models A-D for service sires (n=306) are reported in Table 2, above the diagonal. Model A was the closest to RCR estimates, giving rank correlation of 0.84, while solutions from models B, C, D were less related (0.77/0.76/0.74, respectively). Estimates obtained in A case where in any case similar to those obtained by models B, C, and D (0.97/0.97/0.98, respectively). The three latter models gave essentially the same estimates (0.99). Solutions for the service sire permanent environmental effect from model F showed the same pattern of solutions from model A, and the correlation between models A and F solutions was 0.98. Below the diagonal are reported the rank correlations between the solutions of those sires being both service sires and sires of service sires (n=48). Correlations between solutions from models A-D and RCR followed the same pattern discussed above, although a bit lower (except between models B, C, D). Solutions for models E and F solutions were not related to RCR (0.06 and -0.01), and very poorly related to models A, B, C, D solutions. Correlations between models E and F solutions were medium (0.78).

The variance due to the service sire, both environmental (models A and F) and additive genetic (models B, C and D) was low and didn’t vary significantly across models. Despite this, heritability for direct effect on fertility at the embryo level was around 7%, higher than other estimates found in literature (Jansen, 1986; Andersen-Ranberg et al., 2003), but lower than the estimate of Nadarajah et al. (1988). The proportion of variance due to the service sire as permanent environmental effect both from model A and F is similar to what reported by Jamrozik et al. (2005) and higher than results from Weigel and Rekaya (2000). The inclusion of maternal environmental (cow) and additive genetic (sire of cow) effects didn’t really affect the variance components for the direct effect. Rank correlation showed that models B, C and D give the same estimates of service sires solutions, while there is a moderate re-ranking if the relationship matrix was not included (model A). Re-ranking was larger if service sires were evaluated by RCR. Models A, B, C and D gave similar estimates of variances and sire solutions, which came out to be quite different if the sires were ranked for their RCR. Thus, differences in estimate of the service sire conception rate are likely to come out when a prediction model is applied, rather than including a relationship matrix among the service sires. If the additive genetic effect is reported to the sire of the service sires (sire paternal effect in the sire model context), heritability is lower (4.2%), and strongly decreases when the permanent environmental effect of the service sire is added (0.9%). The latter is closer but higher than the estimates of Hyppanen and Juga (1998). Moreover, solutions for the service sire paternal effect seem to be scarcely concordant with the solutions for the service sire fertility on the embryo level (models E and F vs. models A-D, Table 2), and between the solutions from the same model if the service sires permanent environmental effect is added (model E vs. model F, Table 2). Comparing models A and F, which both consider service sire as environmental effect, the rank correlation between solutions is 0.98, meaning that service sires don’t really differ in CR if considered averaging for their genetic merit.

Conclusions

The aim of study was to investigate different model structures for the evaluation of dairy bulls for male fertility. The dataset used was extracted by a unique dataset concerning single inseminations records performed on Brown Swiss heifers and cows reared in the Eastern Italian Alps. The six different models we constructed gave similar variance components for the service sires effect but a different ranking of the sires. The main differences were found comparing the Raw Conception Rate and the solutions from the prediction models, and, among these models, bulls re-rankings were found when inseminations were related to the service sire (embryo survival) or to the sire of the service sire (service sire semen fertility). The latter comparison may suggest that the embryo survival and the service sire semen fertility are different traits and not genetically related. Phenotypic and genetic differences in male fertility among the service sires exist, and should be monitored thought a reliable evaluation system. Predictive ability of the different models should be evaluated in order to find the most reliable prediction model of service sire fertility.

References


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