Original article

Genetic parameters for twinning in the Maine-Anjou breed

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Summary – Genetic parameters and bull transmitting abilities were estimated for twinning in the Maine-Anjou breed. Twin calving performance was analyzed as a threshold binary trait assuming direct and fetal effects and polygenic inheritance. The statistical model included the effects of parity, year-season, herd, sire of the fetus, sire of the cow and cow within sire. Heritabilities were 0.13 and 0.02 for direct and fetal effects, respectively, with a correlation between both effects of 0.36. Transmitting abilities of bulls were expressed on the underlying and observed scales; the bull ranked first had an observed twinning rate of 13.7% among its 259 female progeny, corresponding to an estimated breeding value of 2.6 units of underlying standard deviation or 13.9% as the probability for a future daughter to have a twin calving in her second parity. It is concluded that there is considerable place for twinning selection among Maine-Anjou bulls.

cattle / twinning / genetic parameter / sire evaluation / threshold model

Résumé – Paramètres génétiques de la gémellité en race Maine-Anjou. *Cette étude vise à estimer les paramètres et les valeurs génétiques de la gémellité en race bovine Maine-Anjou. L'analyse du taux de vêlages gémellaires a été effectuée en traitant ce caractère comme un caractère tout-ou-rien à seuil soumis à des effets directs et fœtaux en postulant une hérédité polygénique. Les facteurs de variation pris en compte étaient le rang de vêlage, l'interaction (année × saison de vêlage), le troupeau, le père du fœtus, le père de la vache et la vache intra-père. Le coefficient d'héritabilité a été estimé à 0,02 pour les effets fœtaux et 0,13 pour les effets directs avec une corrélation de 0,36 entre les deux. Les valeurs génétiques transmises des taureaux ont été prédites sur l'échelle sous-jacente. Le meilleur taureau a un taux brut de gémellité de 13,7% sur 259 filles ce qui correspond à une valeur génétique estimée de 2,6 unités d'écart type de valeur génétique transmise au-dessus de la moyenne sur l'échelle sous-jacente ou à une probabilité de 0,139 d'obtenir un vêlage gémellaire en deuxième mise bas chez une future fille. On conclut à l'intérêt d'une sélection sur la gémellité en race Maine-Anjou basée sur les mâles.*

bovin / gémellité / paramètres génétiques / évaluation des reproducteurs / modèle à seuils

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INTRODUCTION

Twinning may have both positive and negative effects on beef cattle production. Detrimental effects of twinning are: calf size reduction, higher stillbirth rates, the production of infertile females and more retained placentas under standard management (Cady and Van Vleck, 1978; Dickerson *et al*, 1988). On the other hand, twinning increases birth and weaning weight ouput per cow calving (Davis *et al*, 1989). The overall twinning effect on beef production may be positive in terms of economic efficiency if twinning rate is high (Dickerson *et al*, 1988). However, twinning is rare in cattle, with only a few populations surpassing a 5% rate. Embryo transfer techniques (Davis *et al*, 1989; Johnson *et al*, 1989) have been applied in order to improve twinning rates but, as pointed out by de Rose and Wilton (1988), transferred embryo survival rates should be improved for application in the commercial beef industry. Genetic selection represents another way, not antagonistic to reproductive techniques, for improving twinning rates. It has been suggested that twinning in cattle could be genetically determined by major genes (Morris and Day, 1986, 1990). If this were the case, genetic improvement could be facilitated with respect to classical selection of a polygenic inherited trait by a rapid fixation of the desired genotype at the major locus (Le Roy, 1989). So far, however, no evidence of a major determining twinning rates in cattle has been found (Syrstad, 1984; Gregory *et al*, 1990). In this article, polygenic inheritance is assumed and two important aspects of genetic selection for twinning in the French Maine-Anjou breed are discussed: genetic parameter estimation and sire genetic evaluation.

MATERIALS AND METHODS

Data

Data were collected by the UPRA Maine-Anjou between 1972 and 1990 in French beef herds. This breed has consistently shown high twinning rates: 5.3% in Ménissier and Frebling (1975), 4.7% in Foulley *et al* (1990; unpublished mimeo). Twinning was coded as 0 (single) or 1 (multiple birth). Editing of data required the sire of fetus, the sire of the cow and the cow to be known for each birth. Two data files were used: data file 1 was used for genetic parameter estimation and it was limited to bulls having at least 20 births as sire of fetus or as sire of cow. Data set 2 was used for genetic evaluation of all bulls. The description of both data files is presented in table I.

It was assumed that the discrete observations 0 or 1 are determined by an underlying normally distributed variable as in Gianola and Foulley (1983). A vector μ of liability means corresponding to subpopulations determined by combinations of levels of fixed $\boldsymbol{\beta}$ and random $\mathbf{u}$ factors was modelled as:

$$\boldsymbol{\mu} = \mathbf{X}\boldsymbol{\beta} + \sum_{i=1}^{5} \mathbf{Z}_i \mathbf{u}_i \qquad [1]$$

Table I. Description of data sets analyzed.

	Data set 1	Data set 2
Number of births	65 566	82 798
Twinning rate (%)	5.03	5.04
Sires of fetuses	706	3 438
Sires of cows	719	2 939
Total bulls	1 109	4 445
Cows	25 704	31 683
Herds	1 449	1 654
Year-seasons [a]	73	73
Parities[b]	1-10	1-10

[a] Seasons defined as: 1) January-February, 2) March-May, 3) June-September and 4) October-December; (b) Later parities included as parity 10.

where:

$\boldsymbol{\mu}$: vector of underlying means

$\boldsymbol{\beta}$: vector of parity of cow effects

$\mathbf{u}_1$: vector of sire of fetus effects

$\mathbf{u}_2$: vector of sire of cow effects

$\mathbf{u}_3$: vector of cow within sire of cow effects

$\mathbf{u}_4$: vector of herd effects

$\mathbf{u}_5$: vector of season by year effects

$\mathbf{X}$ and $\mathbf{Z}$: incidence matrices.

The $\mathbf{u}$ effects had null means and (co)variances:

$$\text{Var}\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{u}_3 \\ \mathbf{u}_4 \\ \mathbf{u}_5 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_1^2 & \mathbf{A}\sigma_{12} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{21} & \mathbf{A}\sigma_2^2 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_3^2 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_4^2 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_5^2 \end{bmatrix} \qquad [2]$$

where:

σ_1^2: sire of fetus variance

σ_2^2: sire of cow variance

σ_{12}: sire of fetus-sire of cow covariance

σ_3^2: cow within sire of cow variance

σ_4^2: herd variance

σ_5^2: season by year variance

$\mathbf{A}$: additive relationship matrix among bulls

$\mathbf{I}$: identity matrix.

Herd and year-season effects represent many environmental factors such as nutritional levels, reproductive management, temperature and day length whose

effects on twinning rates were reviewed by Morris and Day (1986). Parity has a well known effect on twinning, wiht heifers showing smaller rates than cows (Manfredi *et al*, 1990a).

Twinning can be roughly regarded as a synthesis of multiple ovulation, fertility and embryo survival. The cow and the sire of cow effects in model [1] can be used to quantify the genetic variation of a complex trait combining multiple ovulation, female fertility and embryo survival. The sire of fetus effect measures the genetic component of a combination of male fertility and embryo survival. In terms of the fetal model, as described by Van Vleck (1979; unpublished mimeo), the sire of fetus and sire of cow (co)-variances in [2] can be expressed in terms of fetal and direct effects as:

$$\sigma_1^2 = \frac{1}{4}\sigma_f^2$$

$$\sigma_2^2 = \frac{1}{16}\sigma_f^2 + \frac{1}{4}\sigma_d^2 + \frac{1}{4}\sigma_{fd}$$

$$\sigma_{12} = \frac{1}{8}\sigma_f^2 + \frac{1}{4}\sigma_{fd}$$

$$\sigma_3^2 = \frac{3}{16}\sigma_f^2 + \frac{3}{4}\sigma_d^2 + \frac{3}{4}\sigma_{fd} + \sigma_p^2$$

where:

σ_f^2: additive genetic variance of fetal effects

σ_d^2: additive genetic variance of direct effects

σ_{fd}: genetic covariance between direct and fetal effects

σ_p^2: variance of permanent environmental effects.

Note that vector $\mathbf{u}_1$ (sires of fetuses) represents transmitting abilities of fetal effects. The vector $\mathbf{u}_2$ (sires of cows) represents transmitting abilities for direct effects plus one quarter of fetal effects. The nonnull covariance between sire of fetus i and sire of cow j is:

$$\mathrm{Cov}\ (u_{1i},\ u_{2j}) = \mathrm{Cov}\ (\frac{1}{2}f_i,\ \frac{1}{4}f_j + \frac{1}{2}d_j)$$

$$= \frac{1}{8}a_{ij}\sigma_f^2 + \frac{1}{4}a_{ij}\sigma_{fd}$$

with a_{ij}, an element of the relationship matrix used in [2].

The model described in [1] and [2] could be further improved by considering (co)variances among cow effects *via* the relationship matrix among females. Also, non-zero covariances among herd and among year-season effects could have been considered. However, with these modifications, the estimation of location and dispersion parameters would have been very difficult. It should be noted that model [1-2], in spite of some simplifying assumptions, remains one of the most complete model applied to twinning field data so far.

Methods

Solutions for the location parameters of model [1] were obtained by the method of Gianola and Foulley (1983). Variance components were estimated by the "tilde-hat approach" of Van Raden and Jung (1988), adapted to this non-linear situation with correlated random factors as in Manfredi *et al* (1991).

RESULTS AND DISCUSSION

Underlying solutions for parity effects, expressed as units of the residual standard deviation and as adjusted percentages, followed closely the observed percentages (table II, fig 1). As expected, the heifer twinning rate represents less than half of the cow twinning rates; also, there is a consistent upward trend across parities of cows. This evolution of twinning rate across parities was also found in other breeds (Johansson *et al*, 1974; Maijala and Syväjärvi, 1977). The difference between extreme solutions for parity effects was 0.59 σ_e (or 6.03%) thus reflecting the importance of this factor on twinning.

Table II. Observed and estimated twinning rates across parities in Maine-Anjou cattle (data set 1).

Parity	n	Observed percentage	Adjusted percentage	Underlying solution[a]
1	20 945	2.71	2.50	−0.38
2	14 229	5.45	5.05	−0.06
3	10 562	5.94	5.48	−0.02
4	7 681	6.51	6.06	0.03
5	5 186	6.63	6.18	0.04
6	3 202	7.37	6.81	0.09
7	1 916	5.64	5.16	−0.05
8	1 037	6.85	6.30	0.05
9	527	9.11	8.53	0.21
10	281	7.12	6.68	0.08
Overall	65 666	5.03	5.71	1.58

[a] Solutions expressed in units of the underlying residual standard deviation, negative signs indicating less propensity to twinning.

Estimated variance components (table III) indicate that cow and sire of cow effects considerably influence twinning. Variances corresponding to herds, sires of fetus and year-season combinations are smaller. Particularly low is the sire of fetus variance thus indicating that the genetics of the fetus plays a secondary role in twinning. This fact is reflected in the near zero estimate of underlying heritability for fetal effects, result in agreement with the study of Johansson *et al* (1974). The heritability of direct effects of 0.13 is within the range of previous estimates (0.10 by Ron *et al*, 1990; 0.15 to 0.31 by Syrstad, 1984; 0.12 by Manfredi *et al*, 1990a). Applying the usual formula of Dempster and Lerner (1950) with an incidence of
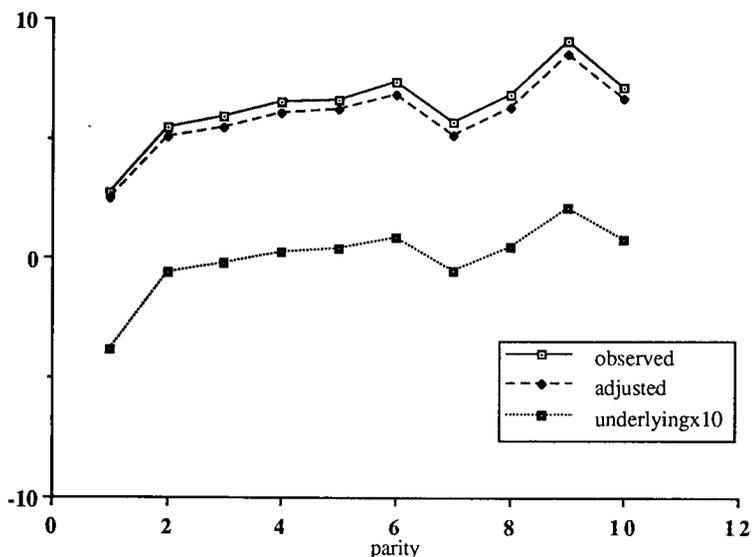
Fig 1. Observed percentages, adjusted percentages and underlying solutions (units of residual standard error × 10) for parity effects on twinning (data set 1).

$P = 5\%$, this value of 0.13 corresponds to a rather low estimate of heritability on the binary scale of 0.03 which is similar to those reported by Cady and Van Vleck (1978) and Maijala and Osva (1990). The moderate but positive correlation between direct and fetal effects may indicate that favorable genes for embryo survival and male fertility are not antagonistic to propensity for twinning.
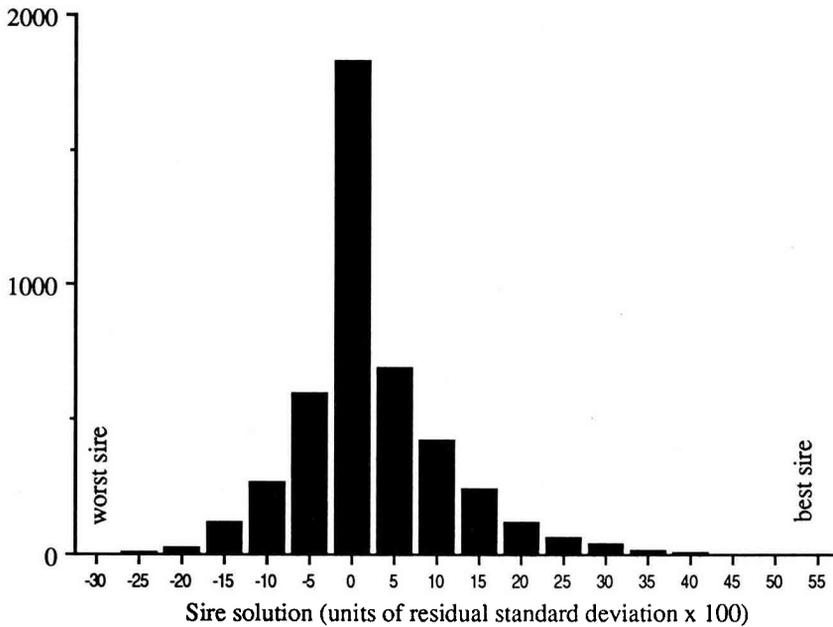
The distribution of solutions for the sire of cow effect is presented in figure 2. The distribution in figure 2 is not normal according to Kolgomorov's test; however, it is bell-shaped and clearly unimodal. This result was also found by Syrstad (1984) and Ron *et al* (1990) who concluded that a polygenic action on twinning is likely; however, the latter authors did not exclude the possibility of a major gene action. The distribution of cow solutions is illustrated in figure 3. Departure from normality is much more important than in figure 2; 84% of the cow solutions are very close to zero. These many solutions near zero reflect the data: many cows have only 1 or 2 records which are often single births. Another important departure from normality in figure 3 is an apparent bimodality which might be in conflict with the assumption of polygenic inheritance made here. However, other factors may act since solutions in figure 3 represent fractions of fetal and direct additive genetic values of cows deviated from the corresponding values of their sires, plus permanent environmental components. Also, the accuracy of solutions in figure 3 is low due to the scarcity of information on each cow.

In fact, inspection of figures 2 and 3 does not allow to draw conclusions on the genetic determinism of twinning. Under a major gene simple hypothesis (1 locus with 2 alleles), at least 3 factors interact for determining the shape of the distribution of estimated genetic values: the allelic frequencies, the interaction between alleles (dominance or additivity) and the magnitude of the genotypic

Table III. Estimated (co)-variances and genetic parameters for twinning in the Maine-Anjou breed (data set 1).

(Co)-variances [a]	
Sire of fetus	0.005
Sire of cow	0.044
Sir of fetus-sire of cow	0.007
Cow within sire of cow	0.086
Herd	0.018
Year-season	0.001
Fetal	0.019
Direct	0.154
Fetal-direct	0.019
Phenotypic	1.154
Heritabilities	
Fetal	0.019
Direct	0.133
Correlations	
Fetal-direct	0.361
Sire of fetus-sire of cow	0.472

[a] Attained convergence 9×10^{-5}. (Co)-variances expressed in units of the residual variance on the underlying scale.

Fig 2. Distribution of solutions for the sire of cow effect (data set 2; $n = 4445$).
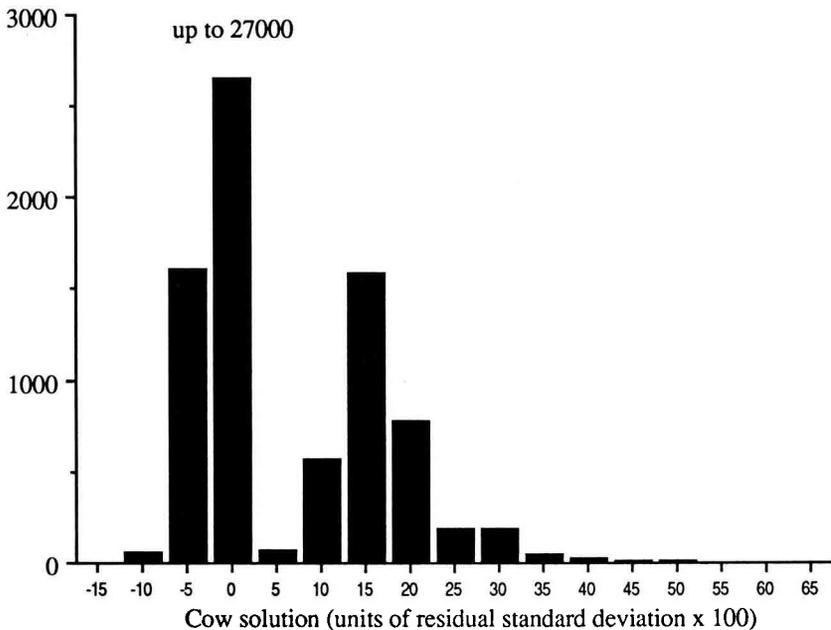
Fig 3. Distribution of solutions for the cow within sire of cow effect (data set 2; $n = 31\,683$).

effects at the major locus on the phenotype. As an example, consider 1 locus under dominant action; the chance of detecting a bimodality would be high when allelic frequencies are intermediate and genotypic effects are large. However, due to chance (sampling), quite large genotypic effects at the major locus would not have been reflected in the distribution of estimated genetic values if allelic frequencies are sufficiently extreme. On the other hand, under polygenic inheritance, one could conceive a non-normal distribution of estimated genetic values due to a lack of fit of the model. In the particular case of twinning, non-registered superovulation treatments could induce a departure from normality. Another factor to be considered is the regression of estimated transmitting abilities of sires or "most probable producing abilities" of cows towards the mean(s) of some population(s). In all analyses assuming polygenic inheritance, major genotypes are ignored when defining such populations. In this study, solutions corresponding to animals with hypothetical different genotypes at the major locus are regressed to the same mean when they should be regressed towards different genotypic means if major gene inheritance holds.

Thus, it would be risky to draw conclusions about the genetic determinism of twinning from simple descriptions of estimated genetic values. Adequate statistical tests should be used in order to reject the polygenic hypothesis (Le Roy, 1989).

Foulley *et al* (1990; unpublished mimeo) proposed a selection program for twinning in the Maine-Anjou breed which should be effective under both genetic hypotheses. Briefly, the program consists of mating the best progeny-tested bulls

to a nucleus of cows having at least 2 multiple calvings. Bull genetic evaluation represents a key aspect of the program; results corresponding to 4 Maine-Anjou bulls are detailed in table IV. The best sire, Liran, was evaluated on 259 daughters with 452 births, 13.7% of them being multiple. Liran was evaluated at 2.6 units of the underlying sire standard deviation or 13.9% which represents the probability for a future daughter to have twins in her second parity when all other conditions are averaged. The comparison between the best bull, Liran, with the second ranked bull, Vano, indicates that rough percentages are not good indicators of genetic merit because they do not take into account the different usage of bulls across environments neither the number of daughters per bull. The contrast between Liran and the worst bull, Beleau, is striking; it seems that there is considerable opportunity for selection among Maine-Anjou bulls. This is also reflected by the value of the standard deviation of the sire of cow transmitting ability of $(0.13 \times z^2 \times 0.05 \times 0.95)^{1/2} = 1.9$ points on the underlying scale corresponding to a coefficient of variation of 38%. This result emphasizes the value of progeny testing bulls on daughter groups in order to increase twinning rate by genetic means as proposed by, among others, Johansson et al (1974), Stolzenburg and Schönmuth (1988) and Gregory et al (1990).

Table IV. Sample of Maine-Anjou bulls evaluated for twinning rate.

	Liran	Vano	Dinard	Beleau
Daughters	259	59	463	171
Births	452	219	1 214	1 396
Observed %	13.7	16.5	2.06	2.51
Genetic index				
Underlying scale [a]	2.6	2.2	−1.4	−1.5
Observed scale [b]	13.9	12.1	2.8	2.6
Repeatability (%)	89	79	86	88

[a] Units of sire standard deviation of the underlying scale; [b] Percentages, with reference to cows having their second calving under average environmental conditions.

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