

# Genetic variability in milking speed of dairy goats

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## Summary

The present investigation deals with the genetic variability of milking speed, measured as the volume of milk collected during the first minute of milking (MD1), and its association with dairy traits. Data originated from 2589 lactations of 1421 Alpine goats, sired by 93 bucks, measured between 1985 and 1997 at the Moissac Goat Experimental Station (Lozère, France). Two genetic analyses were carried out. Firstly, a polygenic model was used to estimate genetic and phenotypic parameters among milking speed and dairy traits using a multiple-trait animal model. Secondly, segregation analysis was used to test the hypothesis of mixed model inheritance (polygenes + major gene) for MF1. Heritability and repeatability of MF1 under the polygenic model were high (0.65 and 0.82, respectively). Estimated genetic and phenotypic correlations between milking speed and dairy traits were low, positive for yields and negative for contents. Segregation analysis yielded a highly significant likelihood ratio, confirming the segregation of a major gene with two alleles with partial dominance. The difference between the mean values of the two homozygotes was around 2.3 phenotypic standard deviation units of the trait. The major gene explained more than 60% of the estimated total genetic variance. The estimate of the 'residual' heritability, after taking into account the effect of the major locus, was 0.30.

## 1. Introduction

Milking speed is an important economic trait because milking time may represent between 40% and 50% of labour time in dairy goat herds (Le Mens, 1974). Moreover, labour time is particularly critical in goat farms processing cheese (about 40% of goat farms in France), where farmers must undertake herd management but also cheese production and marketing. Also, the average size of herds under milk recording increased from 60 to 110 goats during the last 10 years in France. Milking time depends on many environmental conditions (milking parlour, milking machine parameters) and also on the ability of animals for milking. The hypothesis of a major locus contributing to milking speed was postulated by Ricordeau *et al.* (1990) who classified sires into three groups according

to milking speed of their mates and daughters. The first group gave only daughters with low milking speed whatever the milking speed of their mates. The second group, mated to high milking speed females, gave daughters only with high milking speed. The third group, mated to high milking speed females, gave daughters with either low or high milking speed. These observations were coherent with the segregation of a biallelic major gene, with a favourable and recessive allele increasing milking speed. The presence of major genes was confirmed by Ricordeau *et al.* (1990) and Le Roy *et al.* (1995) but there was disagreement between these studies on the degree of dominance at the major gene locus.

The purpose of this study was to estimate the genetic association between milking speed and dairy traits included in the current French selection objective, using a multiple trait polygenic approach, and to revisit the inheritance of milking speed in the Alpine dairy goat by using a single trait segregation analysis.

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## 2. Materials and methods

### (i) Data

Data were collected at the Moissac Goat Experimental Station (Lozère, France). In this herd, artificial insemination was used on about 50% of the herd each year, the semen being chosen according to genetic merit on dairy traits; female replacement was internal and did not include daughters of first kidders. Culling for low milk production was occasionally practised but within-herd systematic selection was not performed. Each year, inseminations and matings started in July and finished in October and kiddings were spread from November to March. Goats were recorded monthly for dairy traits (milk yields and protein and fat contents). The measure used to characterize milking speed was the volume of milk collected during the first minute of the morning milking (MF1). Milking was conducted at a vacuum level of 38 kPa, pulsation rate of 90 pulse/min and pulsation ratio of 2/1. Measurements of milking speed were practised in April over all years, i.e. MF1 was measured only once at each lactation, the trait having a high repeatability within lactation (0.71; Ilahi *et al.*, 1999).

A first data set was edited and analysed in 1997 to study the genetic association between MF1 and dairy traits. This first data set included 2598 terminated lactations of 1457 Alpine goats, born from 125 sires and 754 dams, and recorded from 1985 to 1996. Dairy traits (milk, protein and fat yields, and protein and fat contents) were computed on a total lactation basis from monthly milk recording. In this data set, no restriction was made on the number of daughters per sire, which was five on average. Yields were adjusted to 250 days of lactation length, as in the French official genetic evaluation where lactations longer than 250 days are truncated and lactations shorter than 250 days are extended (Institut de l'Élevage, 1993). Dairy traits were treated as in the official selection scheme because our objective is to estimate genetic correlations between MF1 and traits under current selection.

A second data set was edited and analysed in 1998 to determine the mode of inheritance of MF1 and included 2493 measurements of MF1, corresponding to 1421 goats, born from 93 sites and 760 dams, and recorded from 1985 to 1997. In these data, the sample was restricted to the sire families comprising at least five measured half-sibs to reduce misclassification of genotypes of sires in the segregation analyses.

### (ii) Statistical analyses

Preliminary least squares analyses were conducted for the different traits using the GLM procedure of SAS (1996) to assess non-genetic effects to be included in

the final models. The combined effect of year-season of kidding-lactation number (first, second, third or later lactations) was significant on all traits ( $P < 0.01$ ) for both data sets. There were 79 classes in the first data set and 82 in the second data set. This combined effect allowed for an indirect adjustment of lactation stage for milking speed, which was measured at a fixed date for all animals each year. Also, the season of kidding provided an indirect adjustment of age within first lactation since month and age at kidding were confounded due to seasonal reproduction.

(a) *Estimation of genetic parameters using a polygenic model.* The multiple trait animal model used to estimate heritabilities, repeatabilities and genetic and phenotypic correlations among milking speed, yields and contents was:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{Q}\mathbf{pe} + \mathbf{e},$$

where  $\mathbf{y}$  is the vector of  $n$  observations for all traits  $t$  and for recorded animals,  $\mathbf{b}$  is a vector of fixed effects (year-season of kidding-lactation number, for all traits),  $\mathbf{a}$  is a random vector of genetic animal effects,  $\mathbf{pe}$  is a random vector of permanent environmental effects,  $\mathbf{e}$  is a random vector of residual effects, and  $\mathbf{X}$ ,  $\mathbf{Z}$  and  $\mathbf{Q}$  are incidence matrices relating records to their respective effects. Incidence matrices were identical for all traits. Assumptions of the model are:

$$E(\mathbf{a}) = E(\mathbf{pe}) = E(\mathbf{e}) = \mathbf{0},$$

$$E(\mathbf{y}) = (\mathbf{I} * \mathbf{X})\mathbf{b},$$

with variances and covariances:

$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} * \mathbf{G} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_n * \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_n * \mathbf{R} \end{bmatrix}$$

and

$$\text{Var}(\mathbf{y}) = \mathbf{Z}\mathbf{A}\mathbf{Z}' * \mathbf{G} + \mathbf{Q}\mathbf{I}_n\mathbf{Q}' * \mathbf{P}' + \mathbf{I}_n * \mathbf{R}$$

where: \* denotes the direct product between two matrices;  $\mathbf{A}$  is the numerator relationship matrix among the animals;  $\mathbf{G}$ ,  $\mathbf{P}$  and  $\mathbf{R}$  denote variance-covariance matrices among the six traits for the additive genetic, permanent environmental and residual six effects, respectively; and  $\mathbf{I}_i$  and  $\mathbf{I}_n$  represent identity matrices. All covariances among  $\mathbf{a}$ ,  $\mathbf{pe}$  and  $\mathbf{e}$  are assumed to be null.

The pedigree used for construction of the relationship matrix (2480 animals) traced back two generations of parents of females with data, excluding parents without data and a single progeny. Estimates of genetic parameters for the six traits were obtained by restricted maximum likelihood (REML) with the multiple trait MTC program developed by Misztal (1993), using the expectation-maximization (EM) algorithm. Iterations were stopped when the average squared relative differences for consecutive solutions for  $G$ ,  $P$  and  $R$  were lower than  $10^{-6}$ .

(b) *Segregation analysis.* The segregation analysis method was based on the comparison of likelihoods under different transmission models (Elston & Stewart, 1971). The two hypotheses tested were as follows.

(i) *General hypothesis  $H_1$ :* mixed transmission model for MF1. In this case of transmission, a major gene effect is added to the polygenic variation of MF1. We assume that only two alleles *hd* and *+* are segregating and three genotypes can be encountered: *++*, *hd+* and *hdhd*, coded 1, 2 and 3 respectively. The number of parameters to be estimated is eight:  $\mu_1$ ,  $\mu_2$ ,  $\mu_3$ ,  $\sigma_e$ ,  $\sigma_{ep}$ ,  $\sigma_a$ ,  $p_1$  and  $p_2$  ( $p_3 = 1 - p_1 - p_2$ ) where  $p_1$ ,  $p_2$  and  $p_3$  are the genotypic frequencies. These estimated parameters allowed the computation of the 'residual' heritability  $h_1^2$ , the repeatability  $r_1$ , the fraction of total variance explained by the major gene and the degree of dominance  $d$  defined as  $d = (2\mu_2 - \mu_1 - \mu_3) / (\mu_1 - \mu_3)$ .

(ii) *Null hypothesis  $H_0$ :* polygenic transmission model for MF1. This sub-hypothesis of the general hypothesis is given by  $\mu_1 = \mu_2 = \mu_3 = \mu_0$ . From the four estimated parameters,  $\mu_0$ ,  $\sigma_e$ ,  $\sigma_{ep}$ ,  $\sigma_a$ , we can compute the 'total' heritability  $h_0^2$  and the repeatability  $r_0$ .

The likelihoods are computed under both hypotheses  $H_0$  and  $H_1$ . Letting  $l_0$  and  $l_1$  be these likelihoods, the likelihood ratio  $l = -2 \log(l_0/l_1)$  is compared with a threshold  $\tau$ . The mixed transmission hypothesis is not rejected when  $l > \tau$ .

*Hypothesis testing:* the exact distribution of the likelihood ratio is unknown. Usually, a  $\chi_a^2$  test is performed, with degrees of freedom equal to the difference in number of parameters between the general and the null hypotheses. It is known that this rule does not apply in mixture analysis (Titterton et al., 1985).

We thus preferred to perform an empirical test from simulations. The actual available pedigree and performance structure of our experimental goat data were used to generate 1000 replicates under polygenic transmission ( $H_0$ ). The actual available pedigree comprises 2510 animals including 1421 females with records. The rejection threshold at an  $\alpha = 1\%$  level was 30.2 and the tabulated value of a  $\chi_4^2$  distribution at 1% significance level is 13.3. These results highlight the interest in using empirical tests based on true data structures.

To reduce the number of estimated parameters in the segregation analysis, MF1 data were preadjusted for the environmental effects of year-season of kidding-lactation number, by subtracting a general mean and effects estimated by the preliminary least square analyses. Then data were standardized using the average and standard deviation of overall data. Preadjusted data were fitted using a sire-dam model with repeatability where a female mated to two males

was considered as being two different dams. Sires and dams were assumed to be unrelated. This approach based on precorrection of data and partial use of pedigree information, is less complete than alternative methods using Bayesian methodology (e.g. Janss et al., 1995). However, our experience is that this simpler approach is robust and gives useful results.

The estimation of parameters maximizing the likelihoods was carried out by using the Gauss-Hermit quadrature (D01BAF) and optimization (E04JBF) subroutines of the NAG FORTRAN Library with a quasi-Newton algorithm in which the derivatives were estimated by finite differences.

### 3. Results and discussion

#### (i) Estimation of genetic parameters under a polygenic model

Means and standard deviations for each trait are summarized in Table 1. Milking speed (MF1) has a higher coefficient of variation (0.31) than the other traits. MF1 showed a distribution skewed to the right (coefficient of skewness of 0.56) but data were not transformed. False positive may occur in segregation analyses when the data have a skewed distribution; on the other hand, transformed data may hide a true major gene effect.

Estimates of heritabilities, repeatabilities and genetic and phenotypic correlations among milking speed, yields and contents are presented in Table 2. There are moderate heritabilities for milk, protein and fat yields ranging from 0.35 to 0.38, high heritabilities (and repeatabilities) for protein and fat contents (0.75 and 0.72, respectively), negative genetic and phenotypic correlations between milk yield and contents ( $-0.51$  and  $-0.41$ ;  $-0.34$  and  $-0.20$ , for protein and fat contents, respectively) and a high genetic correlation between contents (0.59). These results are in agreement with estimates reported by Barbieri et al. (1995), but heritabilities and repeatabilities are slightly higher than those obtained by Boichard et al. (1989) on French farm data for the Alpine breed.

MF1 has high heritability and repeatability (0.65 and 0.82, respectively). This result is in agreement

Table 1. Means and standard deviations for each trait

| Traits                 | Mean   | SD     |
|------------------------|--------|--------|
| Milking speed (kg/min) | 1.095  | 0.339  |
| Milk yield (kg)        | 722.40 | 186.50 |
| Protein yield (kg)     | 21.30  | 5.60   |
| Fat yield (kg)         | 23.40  | 6.60   |
| Protein content (g/kg) | 29.60  | 2.52   |
| Fat content (g/kg)     | 32.50  | 4.22   |

Table 2. Heritabilities ( $h^2$ ), repeatabilities ( $r$ ), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among milking speed, milk, protein and fat yields, and protein and fat contents in goats: multiple-trait animal model

| Traits          | $h^2$ | $r$  | Milking speed | Milk yield | Protein yield | Fat yield | Protein content | Fat content |
|-----------------|-------|------|---------------|------------|---------------|-----------|-----------------|-------------|
| Milking speed   | 0.65  | 0.82 | —             | 0.10       | 0.01          | 0.03      | -0.13           | -0.07       |
| Milk yield      | 0.35  | 0.54 | 0.08          | —          | 0.75          | 0.57      | -0.51           | -0.34       |
| Protein yield   | 0.33  | 0.52 | 0.05          | 0.88       | —             | 0.70      | 0.18            | 0.05        |
| Fat yield       | 0.38  | 0.56 | 0.06          | 0.76       | 0.81          | —         | 0.06            | 0.57        |
| Protein content | 0.75  | 0.82 | -0.07         | -0.41      | 0.04          | -0.07     | —               | 0.59        |
| Fat content     | 0.72  | 0.81 | -0.01         | -0.20      | 0.02          | 0.46      | 0.48            | —           |

Table 3. Results of segregation analysis on adjusted data set of MF1

| Parameters              | Null hypothesis $H_0$<br>(polygenic model) | General hypothesis $H_1$<br>(mixed model) |
|-------------------------|--|---|
| $\mu_0$ (kg/min)        | -0.027                                     | —   |
| $\mu_1$ (kg/min)        | —  | -0.185                                    |
| $\mu_2$ (kg/min)        | —  | -0.068                                    |
| $\mu_3$ (kg/min)        | —  | 0.392                                     |
| $\sigma_e$              | 0.159                                      | 0.163                                     |
| $\sigma_{ep}$           | 0.162                                      | 0.135                                     |
| $\sigma_a$              | 0.230                                      | 0.140                                     |
| $p_1$ (+ +)             | —  | 0.35                                      |
| $p_2$ ( $hd$ +)         | —  | 0.44                                      |
| $p_3$ ( $hdhd$ )        | —  | 0.21                                      |
| Heritability            | 0.51                                       | 0.30                                      |
| Repeatability           | 0.76                                       | 0.58                                      |
| Degree of dominance (%) | —  | 59  |
| Likelihood ratio        | 68.5                                       |   |

with preliminary estimates of Ilahi *et al.* (1998) based on a subset of the data used in the present study and it is coherent with the hypothesis of mixed-model inheritance proposed by Ricordeau *et al.* (1990) and Le Roy *et al.* (1995). The estimate of repeatability in this study (between lactations) was slightly higher than the estimate of repeatability (within lactation) reported by Ilahi *et al.* (1999).

Genetic and phenotypic correlations between MF1 and milk traits on a total lactation basis were low, positive for yields but negative for contents. These correlations are slightly lower than those estimated by Ricordeau *et al.* (1990): phenotypic correlations between MF1 and milk yield, fat content and protein content of 0.17, -0.06 and -0.11, respectively. They are also lower than correlations between daily milk production and MF1 and maximum flow rate (0.25 and 0.42, respectively) reported by Ilahi *et al.* (1999). However, Peris *et al.* (1996) obtained high correlations between milk yield and MF1, average milking speed and maximum flow rate (0.63, 0.48 and 0.54, respectively).

#### (ii) Segregation analysis of MF1 data

The maximum likelihood estimates of the parameters (for both polygenic and mixed-model hypotheses) for the adjusted data set of MF1 are given in Table 3 (estimates converted from standard units to units of the trait). The likelihood ratio comparing mixed and polygenic transmission models was about 68.5, greatly exceeding 30.2, the 1% empirical rejection threshold from 1000 simulations under the polygenic hypothesis ( $H_0$ ). Thus, the hypothesis of a major gene with two alleles influencing MF1 is more likely than the polygenic hypothesis. The normal allele (+) is partly dominant over the favourable one ( $hd$ ), with a degree of dominance of 0.59. The difference between the mean values of the two homozygotes is around 2.3 phenotypic standard deviation units of the trait. These results are similar to those previously obtained by Ricordeau *et al.* (1990) but not in perfect agreement with another study reported by Le Roy *et al.* (1995), who evoked co-dominance at the major locus between the two alleles,  $hd$  and +.

The frequency of the *hd* allele in the analysed sample was about 0.42 and higher than the estimate by Le Roy *et al.* (1995). The hypothesis of Hardy–Weinberg genotype frequencies [ $f(hd)^2$ ,  $2f(hd)f(+)$  and  $f(+)^2$ ] for *hdhd*, *hd+* and *++* animals, respectively, was tested against the general hypothesis in which the three genotypic frequencies can take any value. The likelihood ratio was very low (0.31) indicating that the three estimated genotypic frequencies of the analysed sample were not significantly different from those expected under the Hardy–Weinberg equilibrium hypothesis and that selection and matings at the Moissac Goat Experimental Station were carried out independently of the genotype at this major locus.

The estimated heritabilities and repeatabilities were lowered from  $H_0$  to  $H_1$ , from 0.51 to 0.30 and from 0.76 to 0.58, respectively. The major locus accounts for 63% of the estimated total genetic variance of MF1, so the genetic determinism of the trait is strongly influenced by the major gene.

#### 4. Conclusion

Our results confirmed the segregation of a major gene influencing milking speed in goats, using an empirical statistical test. The biological background, however, is unknown. The gene could influence morphological characteristics of teats and udders since milking speed is associated with these characteristics (Bruckmaier *et al.*, 1994). Another possibility is related to the physiology of the opening and the tissular organization of the teat sphincter (Marnet, 1996). The eventual role of oxytocin is less clear since the alveolar milk is not very important in goats compared with cisternal milk, which represents 70% of the total milk collected (Delouis, 1981).

The genetic parameters estimated for MF1 indicate a high genetic variation and low correlations between MF1 and dairy traits on a total lactation basis. The high genetic variability of MF1 and the low genetic correlations between this trait and dairy traits indicate that direct selection for milking speed would be efficient and beneficial for improving milking ability in dairy goats. The major gene influencing MF1 could help selection efficiency for milking speed by avoiding the selection of animals having the ‘normal’ allele (low milking speed) at the postulated major locus. However, before proposing selection on milking speed, more research is needed to study the associations between milking speed and other related traits such as udder and teat characteristics and somatic cell counts.

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