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## Genetic parameters for first lactation dairy traits in the *Alpine* and *Saanen* goat breeds

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**Summary** — Genetic parameters for dairy traits in first lactation (milk yield, fat and protein yields, fat and protein contents) were estimated by restricted maximum likelihood in the *Alpine* and *Saanen* goat breeds from records including progeny of 473 and 238 unproven bucks respectively, mainly used in natural mating. The differences between breeds could also be estimated when the flocks used both breeds. The sampling of the data sets, the addition of data from 28 and 22 progenies of AI proven sires, and the relationship matrix between sampling sires contributed to increase the connection level between flocks, which, however, remained rather low. In the same environmental conditions, particularly in the same year-flock, the *Saanen* breed appeared more high-yielding than the *Alpine*, but solid content was lower. Within-breed, the genetic standard deviation was 1.8-2 fold larger for fat content than for protein content. The heritability of fat and protein yields was rather high (0.31 to 0.39). The genetic correlations between yields were larger than 0.8. They were generally negative but rather low (-0.30 to +0.07) between milk yield and contents. They were clearly positive between fat yield and content (0.45 to 0.59), and between protein yield and content (0.14 to 0.29). They were close to zero and possibly positive between the yield of one component and the content of the other (-0.02 to +0.34). Some discrepancies with the average literature data need to be confirmed.

**dairy goat – genetic parameters – breed comparison – fat – protein**

**Résumé** — Paramètres génétiques des caractères de production laitière en première lactation dans les races caprines *Alpine* et *Saanen*. Les paramètres génétiques des caractères laitiers en première lactation (quantité de lait, de matière protéique et de matière grasse, taux butyreux et protéique) sont estimés dans les races caprines *Alpine* et *Saanen* par la méthode du maximum de vraisemblance restreint, avec 473 et 238 descendance de mâles non sélectionnés, utilisés principalement en monte naturelle. Les différences entre races sont estimées dans les élevages utilisant les deux types génétiques. Le choix des échantillons, la prise en compte de 28 et 22 descendance de mâles d'insémination sélectionnés ainsi que des parentés entre boucs à l'aide d'un modèle équivalent, contribuent à maximiser les connexions entre élevages qui restent cependant d'un niveau faible. Comparée dans les mêmes élevages, la race *Saanen* apparaît plus productive que la race *Alpine* mais son lait est moins riche. Intra race, le taux butyreux est génétiquement 1,8 – 2 fois plus variable que le taux protéique. L'héritabilité estimée des quantités de matière est

assez élevée (0,31 – 0,39). Les corrélations génétiques sont supérieures à 0,8 entre quantités. Elles sont généralement négatives mais relativement faibles entre quantité de lait et taux (-0,30 – +0,07). Elles sont nettement positives entre taux butyreux et quantité de matière grasse (0,45 – 0,59) et entre taux et quantité de matière protéique (0,14 – 0,29). De même, les corrélations croisées entre un taux et la quantité de l'autre matière sont encore positives mais assez variables et plus faibles (-0,02 – +0,34). Certaines différences par rapport aux données de la littérature restent à confirmer.

**chèvre – paramètres génétiques – comparaison de races – matière protéique – matière grasse**

## Introduction

The number of dairy recorded goats increased in France from 111,000 in 1982 to 119,000 in 1985. Two-thirds were *Alpine* and one-third *Saanen*. Up to the beginning of the 1980s, the efficiency of the selection scheme remained low because only 10% of the females were artificially inseminated, and the average production level remained unchanged for 10 years. However, the technology of artificial insemination (AI) has now been improved, so that its use is strongly increasing (37,000 inseminated goats in 1987). Because goat milk is exclusively processed into cheese in France, the main selection goal is the protein yield. But as the average protein content is rather low (27 g/kg), with 22% of uncoagulable protein (Grappin *et al.*, 1981), it should be considered as an important secondary selection goal. So this paper deals with the estimation of genetic parameters, which constitutes a preliminary step for a successful selection for protein, especially since the literature for protein traits has been very sparse in the dairy goat, and in all dairy species until recently.

## Materials and Methods

### *Description of the data*

Data were taken from the National Milk Recording files. They comprised the first lactation records with kidding between September 1st 1982 and August 31st 1986, of daughters of registered sires belonging to the main breeds, *Alpine* and *Saanen*. As natural mating was predominant, the connection level between flocks was low. The data samples were then chosen with a view to maximization of the connections.

Three data sets were obtained:

1) The "*Alpine*" females, sired by *Alpine* bucks and born from mainly *Alpine* dams, 3% being *Saanen* or crossbred.

2) The "*Saanen*" females, sired by *Saanen* bucks and born from mainly *Saanen* dams, 15% being *Alpine* or crossbred. From these data sets, the genetic parameters were estimated within breed of sire. Bucks with fewer than 10 daughters were discarded. To avoid bias due to selection, only young unproven sires contributed to the variance components estimation. However, additional data from widely used proven sires, *i.e.* with progeny in 20 flocks, were included to increase connections. Table I summarizes the structure of these data sets which comprised only 15% of the recorded does during this period because of the connection requirements.

**Table I.** Structure and mean performance of the within-breed data sets.

	<i>Alpine breed</i>	<i>Saanen breed</i>
No. of females daughters of:	11856	5744
proven sire	2765	1408
unproven sire	9091	4336
No. of sires:		
proven	28	22
unproven	473	238
No. of ancestors included in the analysis	302	154
No. of year-flocks (YF)	910	459
No. of females:		
per proven sire	98.0	64.0
per unproven sire	19.2	18.2
No. of females per YF	13.0	12.5
No. of sires per YF	3.6	3.2
Means of traits:		
Age at kidding (day)	420	416
Day of kidding (day)	Feb. 22	Feb. 12
Average birth type	1.97	2.02
Lactation length (day)	231	240
Milk yield (kg)	456	512
Protein yield (kg)	12.5	13.6
Protein content (g/kg)	27.6	26.7
Fat yield (kg)	14.7	15.7
Fat content (g/kg)	32.3	30.9

3) The third data sample included the pure-bred females (sire, dam and doe of the same breed) of *Saanen* and *Alpine* breeds, belonging to 200 year-flock groups with both breeds. From this data set, the difference in production level between breeds was estimated in the same environment. Although the average milk production level was lower in this sample than in the whole population (by 26 and 41 kg for the *Alpine* and the *Saanen* respectively), this data set seemed to be adequate for the breed comparison. No difference between breeds appeared in the distribution of ages or origins of the sires (natural mating or AI). Table II summarizes the structure of this data set.

#### *Description of the variables*

The analyzed dairy traits were the following: milk, fat and protein yields, fat and protein contents. Day of kidding and age at kidding were also taken into account in the breed comparison analysis. Yields were partially corrected for lactation length according to the French evaluation system (Poutous *et al.*, 1981; Bonaïti *et al.*, 1984) and to other studies in dairy cattle (Boichard & Bonaïti, 1987) and sheep (Barillet and Boichard, 1987):

Corrected yield = Total yield x 290/(Lactation length + 60).

For rather long lactations (200 days), this corrected yield is about the same as the average daily yield (= Total yield/Lactation length). But for short lactations, the correlation between corrected yield and days in milk remains intentionally highly positive.

**Table II.** Structure and mean performance of the data set used for the breed comparison.

	Alpine breed	Saanen breed	All
No. of females	2863	2054	4917
With fat information	2528	1820	4348
No. of year-flock	200	200	200
With fat information	180	180	180
No. of females per YF	14.4	10.3	24.7
Means of traits:			
Age at kidding (day)	426	417	423
Day of kidding (day)	Feb. 22	Feb. 11	Feb. 17
Lactation length (day)	227	238	232
Milk yield (kg)	447	490	465
Protein yield (kg)	12.2	13.1	12.5
Protein content (g/kg)	27.4	26.8	27.1
Fat yield (kg)	14.2	15.2	14.6
Fat content (g/kg)	31.9	30.9	31.5

### Methods of analysis

The model for the breed comparison included the fixed effects of the breed, the year-flock, the year-month of littering (5 levels per year due to seasonality: autumn, January, February, March, April or later), the age at kidding (6 levels: 11 months or less, 12, 13, 14, 15, 16 or more), the birth type of the doe (*i.e.* the litter size at birth of the doe, with 3 levels: 1, 2, 3 or more) for the dairy traits analysis. The number of kids born from the doe was not available. The analysis of day of kidding and age at kidding considered only the effects of the year-flock, the birth type and the breed.

The within-breed variance components were estimated with the REML procedure described by Meyer (1986). The model was the following:

$$Y = X\beta + ZU + E$$

with  $Y$  the vector of analyzed records;  $X$  the design matrix for fixed effects;  $Z$  the design matrix for random effects;  $E$  the vector, assumed to be normally distributed with zero expectation and variance  $I\sigma_E^2$ ;  $\beta$  the vector of the fixed effects of the year-flock, the year-month, the age at kidding, the birth type (defined as above), the genotype of the dam (*Alpine*, *Saanen* or crossbred) and the sire group (2 levels: old or sampling sires); and with  $U$  the vector of the fixed effects of the old sires or random effects of the sampling sires, assumed to be normally distributed with zero expectation and variance  $A\sigma_S^2$  ( $A$  being the numerator relationship matrix between bucks). The mixed model equations (MME) were the following:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + kA^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ U \end{bmatrix} = \begin{bmatrix} X'Y \\ Z'Y \end{bmatrix}$$

with  $k = \sigma_E^2 / \sigma_S^2$ .

After absorption of the fixed effects, the relationships between bucks were taken into account by setting an equivalent model (Meyer, 1987):

$$(Z^* H Z^* + k I) U^* = Z^* H Y$$

with:  $H = I - X(X'X)^{-1}X'$

$Z^* = ZL$ , with  $L$  a lower triangular matrix such that  $L'L = A$

$U^* = L^{-1}U$ .

$L$  was obtained with the procedure described by Quaas (1976). The pedigree information was restricted to 2 generations of ancestors. Only those ancestors which improved the connection level between sampling bucks were considered.

As the design matrices were equal for all the traits, a transformation to the canonical scale reduced the multivariate analysis to 5 univariate analyses (Meyer, 1985). The tri-diagonalisation of the MME with Householder transformations (Golub and Van Loan, 1982) eliminated the need for the inverse computation (Smith and Graser, 1986) for each trait and at each iteration. Prior estimates were obtained from Henderson's method 3 (1953). Iterations were continued until relative change in each sire component remained < 0.01%. Convergence was achieved in 8 or 9 iterations. Asymptotic standard errors of variance components were derived from the information matrix.

## Results

### *Differences between breeds*

The results are shown in Table III. The *Saanen* goats kidded 8 days earlier and younger than the *Alpine*, and therefore their lactations were 9.5 days longer, due to the seasonality of goat production. After correction for lactation length, milk, fat and protein yields were respectively 54.7, 1.26 and 1.28 kg higher in the *Saanen*. On the other hand, *Alpine* milk was significantly more concentrated: +0.49 g/kg for protein content, +1.13 g/kg for fat content. These differences were important since they reached  $\approx 0.8$  within breed genetic standard deviation for yields and 0.5 for contents.

### *Environmental effects*

Month within year, age at kidding, breed of the dam and birth type significantly affected the yield traits and sometimes the contents. A birth type of 2 or 3 for the female had a negative effect on its milk yield (-9 kg) but no effect on contents. The age at kidding had

**Table III.** Estimates of differences between breeds.

Traits	Unit	Difference Saanen-Alpine	Sampling error
Date of 1st kidding	day	-8.3	0.95
Age at 1st kidding	day	-7.8	1.9
Lactation length	day	9.5	1.5
Milk yield	kg	54.7	3.7
Protein yield	kg	1.28	0.10
Protein content	g/kg	-0.49	0.07
Fat yield	kg	1.26	0.13
Fat content	g/kg	-1.13	0.13

a positive and almost linear effect on yields and a negative effect on contents. A late month of kidding had a strongly negative effect on yields and on contents.

#### *Within-breed of sire genetic parameters*

**Genetic variability of the traits.** The estimates of heritability, genetic and phenotypic standard deviations and genetic coefficient of variation (defined as the ratio of the genetic standard deviation to the phenotypic average of the population given in Table I) are reported in Table IV.

The estimates of heritability were near 0.30 for milk yields, ranged from 0.31 – 0.39 for fat and protein yields and were higher for contents (0.41 – 0.52). For contents, they appeared higher in *Alpine* than in *Saanen*. The estimates were rather high for protein yield in *Saanen* (0.36) and for fat yield in *Alpine* (0.39).

Although content traits had higher heritabilities, they were genetically less variable, since the genetic coefficient of variation reached 4.4 – 5.5% for protein content and 7.7 – 8.3% for fat content against 11.8 – 15.7% for yields. The genetic coefficients of variation were always larger in *Alpine* than in *Saanen*, because of the smaller average production level and of higher genetic standard deviations, especially for contents: 1.51 g/kg in *Alpine* against 1.17 in *Saanen* for protein content, 2.68 g/kg against 2.38 for fat content.

Whereas heritability for fat and protein were about the same, fat appeared genetically more variable than protein, since the ratio of their genetic standard deviations reached 1.8 – 2 for contents and 1.2 – 1.5 for yields. This fact could not be explained solely by a “scale effect”, since it also appeared with the genetic coefficients of variation: 7.7 – 8.3% for fat content against 4.4 – 5.5% for protein content; 12.9 – 15.7% for fat yield against 12.0 – 12.6% for protein yield, according to the breed.

**Correlations between traits.** Phenotypic and genetic correlations between traits are in Tables V and VI for the *Alpine* and *Saanen* breeds, respectively.

The phenotypic correlations between yields and lactation length were positive and moderate (0.32 to 0.43), showing that the correction of yields for lactation length is incomplete. Phenotypic relationships between yields were high (0.87 to 0.95). While pro-

**Table IV.** Estimates of genetic ( $\sigma_g$ ) and phenotypic ( $\sigma_p$ ) standard deviations, of heritability ( $h^2$ ,  $\pm$  sampling error  $\sigma(h^2)$ ) and of genetic coefficient of variation ( $CV_g = \sigma_g/\mu$ ).

Traits	Unit	Alpine					Saanen				
		$\sigma_p$	$\sigma_g$	$h^2$ (%)	$\sigma(h^2)$ (%)	$CV_g$ (%)	$\sigma_p$	$\sigma_g$	$h^2$ (%)	$\sigma(h^2)$ (%)	$CV_g$ (%)
Milk yield	kg	107.2	57.7	29	4	12.7	109.2	60.6	31	6	11.8
Protein yield	kg	2.81	1.55	31	4	12.6	2.76	1.65	36	6	12.0
Protein content	g/kg	2.10	1.51	52	5	5.5	1.84	1.17	41	7	4.4
Fat yield	kg	3.70	2.31	39	4	15.7	3.58	2.02	32	6	12.9
Fat content	g/kg	3.80	2.68	50	5	8.3	3.48	2.38	47	8	7.7

**Table V.** Phenotypic (above diagonal) and genetic correlations (below diagonal) in *Alpine* breed.

	<i>Milk yield</i>	<i>Protein yield</i>	<i>Protein content</i>	<i>Fat yield</i>	<i>Fat Content</i>
<i>Milk yield</i>		0.95	-0.36	0.89	-0.13
<i>Protein yield</i>	0.90		-0.06	0.91	0.01
	±0.04				
<i>Protein content</i>	-0.30	0.14		-0.14	0.45
	±0.10	±0.11			
<i>Fat yield</i>	0.84	0.91	0.06		0.31
	±0.05	±0.04	±0.11		
<i>Fat content</i>	0.07	0.34	0.56	0.59	
	±0.11	±0.11	±0.08	± 0.09	

**Table VI.** Phenotypic (above diagonal) and genetic correlations (below diagonal) in *Saanen* breed.

	<i>Milk yield</i>	<i>Protein yield</i>	<i>Protein content</i>	<i>Fat yield</i>	<i>Fat Content</i>
<i>Milk yield</i>		0.94	-0.35	0.87	-0.17
<i>Protein yield</i>	0.93		-0.05	0.88	-0.05
	±0.05				
<i>Protein content</i>	-0.08	0.29		-0.14	0.43
	±0.19	±0.12			
<i>Fat yield</i>	0.80	0.82	0.19		0.31
	±0.07	±0.07	± 0.15		
<i>Fat content</i>	-0.16	-0.02	0.44	0.45	
	±0.15	±0.20	± 0.12	± 0.14	

tein content appeared negatively correlated with milk yield (-0.36 to -0.38), the opposition between milk yield and fat content was very moderate (-0.13 to 0.17).

Some estimates of genetic correlations were very close to phenotypic correlations. Yields were highly correlated. The strongest correlation was obtained between milk and protein yields (0.90 to 0.93), the weakest between milk and fat yields (0.80 to 0.84), while the correlation between fat and protein yields was intermediate (0.82 to 0.91). Fat and protein contents were less correlated (0.44 to 0.56) than corresponding yields.

Other correlations presented some differences. Contents appeared in moderate opposition with milk yield and the results were not homogeneous between breeds and traits. The correlations ranged from -0.30 between milk and protein content in *Alpine*, to 0.07 between milk and fat content in the same breed. Consequently, all the relationships between matter yields and contents appeared to be positive. The correlation between fat yield and fat content (0.45 to 0.59) was higher than the correlation between protein yield and protein content (0.14 to 0.29). Correlations between fat content and protein yield and between fat yield and protein content were positive or zero (-0.02 to 0.34).

## Discussion

### *Differences between breeds*

The 2 breeds have rather a different production potential. The estimated superiority of the *Saanen* breed confirms the difference between the average production levels in the whole recorded population. Moreover, this difference may be underestimated because the environment is not optimal: the average production level is lower in herds with both breeds than in the whole population, and this loss in productivity is larger in *Saanen* (-41 kg milk) than in *Alpine* (-26 kg). However, this superiority of the *Saanen* in production level is partially balanced from an economic point of view by a greater body weight (which is a disadvantage since a goat has a very low meat value), a lower milk concentration of fat (-1.13 g/kg) and protein (-0.49 g/kg) and by a lower milking speed (Bouillon & Ricordeau, 1981). The estimated differences in sexual precocity and consequently, in lactation length due to seasonality of goat production) are more difficult to discuss, since they may be due to preferential treatment: mating may occur earlier for *Saanen* goats under the assumption that it is practised at a fixed body weight, since the body weight and the growth rate are larger in the *Saanen* than in the *Alpine*.

### *Within-breed genetic parameters*

A review of the literature on estimates of genetic parameters in goats is presented in Tables VII and VIII. The North American studies (Iloeje *et al.*, 1981; Kennedy *et al.*, 1982;

Table VII. Review of heritability estimates of dairy traits in goats.

Authors	Characteristics of the study	Milk yield	Fat yield	Protein yield	Fat content	Protein content
Rönningen, 1967	N=3,003	0.28	0.25		0.28	
	Flocks >10 females	0.36	0.30		0.32	
Steine, 1976	N=17,708	0.72	0.63		0.57	
	3 methods	0.47	0.43		0.45	
		0.33	0.33		0.29	
Ricordeau <i>et al.</i> , 1979	Experimental farm 1st lactations, 100-day	0.64	0.49	0.59	0.62	0.59
Iloeje <i>et al.</i> , 1981	6,452 <i>Alpines</i>	0.49	0.57		0.57	
	1,730 <i>LaMancha</i>	0.61	0.59		0.63	
	6,897 <i>Nubian</i>	0.59	0.64		0.66	
	2,759 <i>Saanen</i>	0.53	0.48		0.62	
	4,007 <i>Toggenburg</i>	0.59	0.59		0.54	
Mocquot and Ricordeau, 1981	N=29,271 1st lactations	0.36	0.22	0.36	0.41	0.48
Sigwald <i>et al.</i> , 1981	N=775				0.52	0.52
Kennedy <i>et al.</i> , 1982	N=3,286	0.68	0.61		0.54	
	1st lactations					
Mavrogenis <i>et al.</i> , 1984	N=1,474 Experimental farm	0.29				
Constantinou <i>et al.</i> , 1985	N=1,600	from 0.29				
	Exp. farm	to 0.35				
Sullivan <i>et al.</i> , 1986	N=2,085 5 breeds	0.46	0.37	0.42		

**Table VIII.** Review of genetic correlation estimates for dairy traits in goats.

Authors	MYxFY	MYxPY	MYxFC	MYxPC	FYxPY	FYxFC	FYxPC	PYxFC	PYxPC	FCxPC
Ronningen, 1967	0.89		0.17				0.52			
Steine, 1976	0.87		-0.28			0.21				
Ricordeau <i>et al.</i> , 1979	0.86	0.95	-0.45	-0.49	0.90	0.07	-0.20	-0.28	-0.19	0.63
Iloje <i>et al.</i> , 1981	0.52		-0.12			0.14				
Mocquot and Ricordeau, 1981	0.75	0.86	-0.39	-0.19	0.78	0.31	0.13	-0.21	0.20	0.64
Sigwald <i>et al.</i> , 1981										0.44
Kennedy <i>et al.</i> , 1982	0.95			0.03		0.32				
Sullivan <i>et al.</i> , 1986	0.93	0.95			0.94					

MY = milk yield; FY = fat yield; PY = protein yield; FC = fat content; PC = protein content.

Sullivan *et al.*, 1986) provided rather high estimates of heritability, which might be inflated by confusion between sires and environmental effects. Other estimates were obtained from an experimental farm (Ricordeau *et al.*, 1979), which may explain the high level of estimated genetic variability. The number of traits analysed varied according to the study. Studies from Cyprus (Mavrogenis *et al.*, 1984; Constantinou *et al.*, 1985) were restricted to the analysis of milk yield (90-day, 150-day or total). Studies from Norway or North America dealt with milk and fat traits. Only the studies of Ricordeau *et al.* (1979), Mocquot and Ricordeau (1981), Sigwald *et al.* (1981), and Sullivan *et al.* (1986) provided estimates for both fat and protein.

Results of Steine (1976) for fat only, and Mocquot and Ricordeau (1981) for fat and protein were obtained from a national dairy recording scheme, with a within-flock analysis, because of the predominant mating system. They generally agreed with the results obtained in the other species, in particular in the dairy cow, as reviewed by Majjala and Hanna (1974) and more recently by Barillet and Boichard (1987). The trends in the literature for the dairy cow may be summarized as follows: heritabilities are smaller for yields than for contents whereas the genetic coefficients of variation, which best represent the possible genetic gain, are higher. Milk yield is generally more heritable than protein or fat yields. Milk and matter yields are highly related, but their genetic correlations with contents are very different: while milk yield is negatively related with contents, and generally more strongly with protein than with fat, the genetic correlations between matter yields and contents are close to zero, except for the correlation between fat yield and fat content, which is clearly positive. Genetic variability is always greater for fat than for protein.

The present estimates do not agree perfectly with these data. This may be due to an unfavourable design. Most of the bucks were used in natural mating. Even after a drastic choice of the data sample and including proven AI bucks and relationships between sampling sires, the connection level remained very low. For example, only 1% of the off-dia-

gonal terms of the sires x sires submatrix ( $Z'HZ$ ) were non-zero after the absorption of the fixed effects.

Some differences appear clearly between our results and the literature data: the genetic opposition between milk yield and contents seemed very moderate or did not exist at all, except for protein content in the *Alpine* breed. Consequently, because of the mathematical relationships, all the correlations between matter yields and contents appeared to be positive, even high for fat yield and content. In the same way, heritability estimates for fat and protein yields were higher than for milk yield, because of the lack of an actual opposition between milk and contents.

The present results would be of course very favourable for genetic improvement programs. However, they were obtained from a rather small data sample in the *Saanen* and the data structure was not perfectly adequate in both breeds. Therefore they need to be confirmed by further investigations.

The stability of the estimates according to the method is noteworthy. The maximum difference between estimates obtained from the REML with and without relationships between bucks was only 0.03 for the heritabilities and 0.04 for the genetic correlations. In the same way, it reached only 0.05 for the heritabilities and 0.06 for the genetic correlations between estimates with REML, and Henderson's method 3.

The heritability of protein content agrees with the homologous data in the dairy cow or ewe, in spite of the influence of the  $\alpha_{S1}$ -casein polymorphism on protein content (Grosclaude *et al.*, 1987). These 2 facts do not exclude each other, according to the low frequency of "high" or "null" alleles in the population. However, the larger estimate in the *Alpine* (0.52 versus 0.41) agrees with the higher frequency of rare and extreme alleles in this breed.

## Conclusion

The present results showed the existence of 2 populations with rather different genetic production levels which represents the genetic gain obtained in about 5 years with an effective selection scheme. They also provided estimates of genetic parameters which were rather homogeneous in both breeds; but some disagreements with the literature data in the other dairy species, particularly the lack of a clear opposition between milk yield and contents, are very surprising. These may be explained by low accuracy of our estimates and by the unfavourable design. Therefore, further analysis will be required in a few years when connections have been considerably increased by the more widespread use of artificial insemination.

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