

## GENETIC IMPROVEMENT OF LITTER SIZE IN SHEEP

J.M. Elsen<sup>1</sup>, L. Bodin<sup>1</sup>, D. François<sup>1</sup>, J.P. Poivey<sup>1</sup> and J Teyssier<sup>2</sup>

<sup>1</sup>INRA Station d'Amélioration Génétique des Animaux. BP27 - 31326 Castanet Tolosan - FRANCE

<sup>2</sup>INRA Unité Zootechnique Méditerranéenne, ENSAM, 34060 Montpellier - FRANCE.

### SUMMARY

Key factors for the efficiency of breeding programs for the improvement of litter size in sheep are presented, followed by a discussion about within-breed selection, crossbreeding and use of major genes. New tendencies concerning research on the optimization of litter size level are also described.

### INTRODUCTION

Litter size (LS) is one of the major components of productivity in sheep. Despite its low heritability coefficient, this trait has a large genetic variability between and within breeds. This variability was clearly demonstrated and evaluated in a number of experiments. It may be used in breeding programs combining additive polygenic differences, breed complementarities, heterosis effects and major gene inheritance.

This paper describes the state of the art concerning genetic improvement of LS in sheep and research developments on the optimization of this trait. Particular references are provided from French results.

### BREEDING METHODS FOR THE IMPROVEMENT OF LITTER SIZE

Three sources of genetic variation coexist : i) within-breed additive variability; ii) between breeds, potentially non additive, differences; and iii) major gene segregation. Bradford (1985) showed their respective usefulness for effecting genetic changes. They are or could be jointly used in global breeding programs. However, for the sake of simplicity, they will be successively described.

#### Within breed selection

It has been well established that litter size is poorly heritable (about 0.10) but highly variable. On the contrary, its coefficient of variation is large. In French breeds, for instance, the mean value of the coefficient of variation is 36.5 % in natural conditions (32 breeds, 633000 ewes), and 42.6% after induced oestrus (15 breeds, 27000 ewes) : Bodin and Elsen (1989). The resulting potential genetic progress reaches on the whole 1 to 2 % a year as for many other traits. This potential was proven in a number of selection experiments as listed by Bradford (1985).

Large scale applications were organised in France in the '70s. French sheep industry is characterized by a large number of breeds (about 40 flock books) and a centralized breeding value evaluation (BVE) performed at the national level under INRA's responsibility. Selection programs designed within breeds are more or less sophisticated (Elsen and Bibé, 1988). The realised genetic progress of a selection program is based first on the consistency and perennality of its organisation, then on the quality of the BVE.

#### Organisation of the selection schemes

The long term example of the Lacaune breed program for LS improvement shows that improving prolificacy in sheep can be successfully organised in farm conditions (Perret *et al.*, 1992). This selection scheme was created in 1975 under the control of the OVITEST co-operative structure. In 1991, 20 farms (7000 ewes) were involved in the scheme. The traits measured in the farms were the natural prolificacy at first lambing and the rearing ability evaluated from 10-30 days lambs growth rate. In addition, growth rate, fatness and conformation of rams were controlled in a performance test station.

Details of the organisation are given in Perret *et al.* (1992). The most important figures in 1991 were the testing of 219 ram lambs in a performance test station with a selection of the best 38 considering dam

BVE, individual performances, semen quality and phenotypic appearance; the progeny testing of 38 rams with careful planning of 3500 AIs, each ram being mated to 90 medium value females spread over 8 different flocks (25-30 recorded ewe lambs/sire); and the classification as "elite" of the 10 rams with positive BVE for prolificacy and rearing ability. Genetic progress was evaluated using an animal model. On average, 0.02 extra lamb per lambing were obtained each year, *i.e.* a mean annual genetic progress of 1.2%.

#### *Breeding value estimation.*

Litter size in sheep has some peculiarities which must be accounted for in an efficient BVE. Most of them were taken into account in the new (1992) French evaluation system.

Genealogical information : The use of an Animal Model (AM) which considers all known genealogical relationships is particularly efficient for LS : its heritability is low and a large increase of the BVE precision is expected from information about relatives. Moreover, exchanges of breeding animals between flocks are most often rare, thus limiting the accuracy of comparisons. Adding genetic relations from ancestry, AM should improve those comparisons and the classification of breeding animals.

Multitrait evaluation : In sheep, females may be fertilized on their natural oestrus or with a hormonal treatment required for artificial insemination. Hormonal treatments affect ovulation number and quality. Natural and artificial oestrus have to be considered as two traits with a genetic correlation estimated at 0.4 (Bodin, 1979). Consequently, INRA set up a multivariate breeding evaluation for this trait.

Discrete traits : Statistical models were proposed (Gianola and Foulley, 1983) for the analysis of discrete traits. They are based on the hypothesis of an underlying normal distribution with fixed thresholds and a variable mean, linearly dependant on fixed (flock, year, season, etc.) and random (sire, ewe., etc.) effects. Few evaluation routines are based on these hypotheses. To our knowledge none of them integrate both the animal model and the underlying normal hypothesis.

A diminution of the strong relationship between the LS mean and variance may be obtained with a first order approximation of the true threshold method where the observations (1,2,3, etc.) are transformed to their Kendall and Stuart (1969) mean normal score estimated at the population level (Poivey *et al.*, 1990).

Biological model : The traditional "herd x year x season" effect widely used in BVE, reflects a part of the identifiable variation of LS in sheep. A careful study of recordable effects is needed before the development of any BVE protocol. In the French BVE (Poivey *et al.*, 1990), a ewe is classified into one of 42 physiological states according to rearing mode (for the first parity only), first lambing age, lambing interval, and number of reared lambs at the previous lambing. Accounting for such a large number of levels in this effect is meaningful only in the animal model framework which insures connection between cells.

#### **Crossbreeding**

Use of differences between breeds is a fast way for increasing productivity. Prolific breeds are not uncommon in sheep with the Romanov, Finn, Chios, Dman, Frisonne, and Border Leicester types. As described by Tchamitchian (1975), a variety of mating systems allows a graduated use of prolific genes : pure breed, simple cross, three way cross... The economical values of such systems were studied for a number of prolific breeds (see Ricordeau, 1975 and 1988, for thorough reviews). The value of Finn F1 females, as compared with pure local stocks, was clearly demonstrated by Land *et al.* (1974), Young *et al.* (1988) and others. In France, a comparison between Romanov, Cotentin, Border Leicester and Finn ewes, and their crosses with Berrichon du Cher sires, proved the advantages of the Romanov types (Ricordeau, 1975; Ricordeau *et al.*, 1976) and the economical superiority of Berrichon du Cher x Romanov F1.

The F1 ewe combines parental complementarities and expresses heterosis. From Ricordeau (1976), Land *et al.* (1974) and Young *et al.* (1988) heterosis on litter size at birth seems quite small and generally non significant. The absence of maternal effect on this trait was also proven in these experiments. More synthetic criteria such as total weaned lamb weight which include lamb survival and growth, are, on the contrary, largely affected by heterosis. Following Moav (1966), it must be emphasised that a large part of this heterotic effect is due to the multiplicative definition of the trait.

A major difficulty of back crossing systems is the simultaneous maintenance of 1 or 2 pure-bred sub flocks as parents of F1 ewes. This is practical only when between flocks exchanges of breeding animals are well organised as for instance in the hill areas of the UK and Ireland. These difficulties justified the numerous developments of composite lines as reviewed by Ricordeau (1988). The majority were created including the Finn genes in the mixture (Cambridge, ABRO dam line, Fingalway, Composite I and II, etc.) Some made use of the Romanov breed. The Hungarian Tetra flock combines both origins. In France, the INRA401, initiated in 1969, is a composite line of 50% Romanov, 50% Berrichon du Cher. The line was considered as a new breed at the 4th intercross generation and closed after 1989. At present, 1400 ewes form the INRA401 nucleus, controlled and selected for litter size (since 1980) rearing ability (since 1985) and meat production traits (since 1989) (Ricordeau *et al.*, 1992).

The dissemination of INRA401 in private industry began in 1980. The general scheme is a 4 generations absorption of F1 Romanov x Local breed using INRA401 sires. At the present time, about 30 000 females, amongst them 5 000 belonging to the 4th absorption generation, are bred on 150 private farms. Table 1 is a rough summary of the national performances control of INRA401 as compared with Romanov and Berrichon du Cher.

Table 1. Mean performances of INRA401 composite line in farm, and of its parental breed.

Breed	Number of adult ewes controlled	Litter size after natural oestrus	10-30 days growth-rate of twins males	30-70 days growth rate of twins males
INRA401	9300	1.93	225 g	316 g
Berrichon du Cher	1600	1.41	236 g	322 g
Romanov	2500	2.81	225 g	260 g

#### Using major genes

The discovery of the Booroola gene in 1980 (Piper and Bindon, 1981; Davis *et al.*, 1982) stimulated a new interest for this type of major variability. Appropriate introgression programs allowing for a fast increase in productivity appeared as an alternative to selection and crossbreeding. The prospect of isolating and analyzing of the major gene DNA sequence and its product opened paths for understanding the genetic control of traits. The Booroola gene itself was imported by a number of countries either for practical applications or as a tool for more fundamental physiological studies.

Five carrier rams were given by Australia to the INRA in 1982 and further copies of the gene were obtained from New Zealand (1986) and the UK (1988). The gene has been introgressed in the Mérinos d'Arles (poorly prolific) and Romanov (highly prolific) breeds. Table 2 gives the number of "pure breed" (at least 7/8 Mérinos d'Arles and 15/16 Romanov) now available. Experiments on the physiological control of OR and the genetic location of the gene made extensive use of animals produced during these introgressions.

Table 2. Number of Mérinos d'Arles and Romanov carriers of the Booroola gene in France

Breed	Sexe	++	F+	FF
Mérinos d'Arles	males	9	frozen semen	7
	females	275	400	50
Romanov	males	3	3	
	females	25	50	

The study of this gene stimulated two further areas of research. How could one isolate other major genes controlling such major genes? How should these be used for animal improvement?

#### Finding new major genes

As summarized in the 2nd workshop on Major genes for Reproduction in sheep, extreme animals as regards prolificacy were observed in different breeds, suggesting a possible segregation of a major gene in these stocks: Romney, Javanese, Cambridge, Belclare, Thoka, Olkuska. From these putative major genes,

only the "Inverdale gene" has been clearly proven to exist (Davis *et al.*, 1991). This X-linked gene was demonstrated by progeny testing successive generations of ram offspring of a highly prolific ewe, screened in the whole Romney controlled population. Efforts are currently being made to test simple genetic hypotheses in other breeds, including the Lacaune prolific strain.

Organising and analyzing the phenotypic information : The major genes cited were discovered after careful observation of the data. The question arose as to whether specific statistical criteria and/or experimental designs could increase the possibility of detection of new genes. Very high values for repeatability and heritability should be considered as first, non robust, indications of major gene segregation (Le Roy and Elsen, 1991). A maximum likelihood theory is available for improving the power and robustness of these studies (Elston, 1980). Nevertheless its application to large and multilooped livestock type populations is not easy, in particular when considering categorical traits such as litter size

The hypothesis of a mixed inheritance (one major gene plus polygenic variation) has been tested on data from the Lacaune sheep population (12376 records from 4975 ewes born from 46 sires and 4141 dams) in which very large LS were found. The model and corresponding software dealt with unbalanced, possibly missing, repeated information from daughters and dams in a nested sire/dam/daughter structure. Preliminary results summarized in table 3 led to the H0 polygenic hypothesis being rejected at the .001 level but gave inconsistent parameters estimation as regards male and female genotypic frequencies.

Table 3. Segregation analysis of litter size in the Lacaune sheep breed.

Parameters	Underlying genotypic means			Coefficients of		Male frequencies		Female frequencies	
	AA	AB	BB	$h^2$	$r$	AA	AB	AA	AB
Values	-0.10	0.56	1.57	0.07	0.08	0.55	0.45	0.88	0

Litter size is easily recorded and screening designs aiming at increasing the frequency of favourable alleles at expected major loci can be very powerful. Booroola and Inverdale genes were discovered after such a screening. Going further, we could suggest systematic progeny testing, on poorly prolific females, of rams suspected to be heterozygous carriers of a major gene after the observation of high variability of previous offspring, or because they were born from the mating of opposite extreme individuals.

Using biological tools : The efficiency of markers for the location of QTL influencing LS has been demonstrated in mice by Spearow *et al.* (1991) who found significant effects of marker loci on hormonally induced ovulation rates in backcrosses between 2 divergent strains. In sheep, the genome mapping project organised under the leadership of New Zealanders will provide the tool for detecting such QTLs.

Besides the systematic screening of the genome using marker maps, the careful study of candidate loci will offer efficient shortcuts. A first category of loci is made of these markers which have been found to be linked to an already known major gene. The systematic test of these markers in different breeds could reveal useful variants of the major gene itself, showing intermediate, profitable, effects on LS. In this category of candidate loci we may include markers found in other species to be linked to QTL influencing LS. A second category of loci is made of candidate genes, the products of which are implied in the regulation of LS. Willmut *et al.* (1990), Spearow (1985), Mulsant *et al.* (1991) gave some indications about possible candidate genes such as gonadotrophins (LH, FSH), inhibitors, growth factors (TGF, EGF, FGF).

#### Using major genes

Teams working with the Booroola gene tried to answer two types of questions : How should it be used in commercial populations? What is its real practical interest for the sheep industry?

Organisation of the breeding scheme : The fundamental attractiveness of major genes is the opportunity, after F1 and back crosses, of mixing in pure-bred animals the general aptitude of the breed plus

the specific value of carriers of the "favourable" allele. The introgression of a major gene may be designed in different ways (Boomarov, 1991) which can be optimized using linear programming (Elsen *et al.*, 1985).

Markers are potentially helpful in two respects. For a more precise and cheaper selection of carrier animals and for a faster recovery of the recipient genome. The first aspect is particularly true for LS genes which are not expressed in males and only after puberty in females. Exciting research on such a marker gene linked to the Booroola Fec locus started as early as 1984 in France with the battery of blood groups and the OLA systems (NGuyen *et al.*, 1992). Some RFLPs were then studied, followed by mini and micro satellites (Montgomery *et al.*, 1991; Drinkwater *et al.*, 1991). Montgomery *et al.* (1993) and Lanneluc *et al.* (1994) finally published linkage groups including Fec. The former provided evidence for linkage of the Booroola gene with 2 microsatellites and 2 RFLPs loci. The latter found a cluster of minisatellite loci closed to Fec and indirectly proved the A blood group to be on the same chromosome. These genes belong to the sheep chromosome 6. The present step involves the use of comparative mapping (the equivalent of the Fec locus should be on the Human chromosome 4q) to search for a closer marker of Fec.

The length of an introgression process could be reduced by selecting, within the group of heterozygous carriers, individuals with the higher proportion of marker alleles specific to the recipient breed (Hospital *et al.*, 1992). Four backcross generations with such a selection are equivalent to 6 generations without selection, 3 are equivalent to 4 and 2 to 3. Thus, we can imagine that it will be possible in the future to introgress a major gene in a non carrier breed within 4-5 years and using small populations. Special attention should be paid to the choice of recipient breed parents to be selected amongst the elite of the breed in order to combine the benefit of the introgression and of the within-breed selection in the same flock.

**Economical significance** : The evolution of successive backcross generations during the introgression of the Booroola gene in Mérimos d'Arles breed in France showed that the performances of future "pure breed" FF or F+ animals cannot be predicted from the observation of the only F1 generation which in this case had a mean OR 50 % higher than in the following generations (table 4). Thus results limited to the F1 are specific to this type and are poor predictors of the economical efficiency of pure-bred carrier ewes.

**Table 4.** Mean OR of one year old F+ and ++ ewes in the Mérimos d'Arles backcross generations.

Generation	1/2	3/4	7/8	15/16
F+	2.92 (n=132)	2.19 (n=77)	1.96 (n=318)	1.94 (n=306)
++	1.21 (n=129)	1.11 (n=102)	1.05 (n=545)	1.04 (n=419)

Major locus genotype x breed interactions limit prediction of future introgressed pure-bred animals value. Piper *et al.* (1985) showed the variability of the Booroola gene effect on OR in different breeds. Table 5 reports OR distributions observed in F+ and ++ ewes belonging to the two introgressed breeds in France.

**Table 5.** Ovulation rate (%) of one year old F+ and ++ ewes in Mérimos d'Arles and Romanov breeds.

Breed	Genotype	1	2	3	4	5	6	7	8	9	10	Mean
Mérimos d'Arles	++	95	5									1.05
	F+	21	66	12	1							1.93
	++	8	42	39	9	2						2.55
Romanov	F+	4	6	10	24	23	17	10	3	2	1	5.05

Finally, it must be emphasised that the practical interest of any major gene must be based on its effects on all productive traits. In a large review of available results mostly obtained on F1 or 1/4 Booroola cross, Davis *et al.*, (1991) concluded a large increase of lamb production but a limited increase in productivity due to mortality and growth rate reduction. In France, a 3-year evaluation of Mérimos d'Arles F carriers was started in 1993. The first results (table 6) indicate a 58 percent gain in total weight of 70 days lambs per

mated F+ ewe as compared to ++ Mérinos d'Arles ewes. However, 33 % of the lambs were artificially reared in the F+ group, thus reducing the profitability of this genotype.

**Table 6.** Comparison between the productivity of pure Mérinos d'Arles (MA), 7/8 ++ (++), 7/8 F+ (F+) and F1 Romanov x Mérinos d'Arles (F1) naturally mated with Ile de France rams. (First results)

Genetic type	MA	++	F+	F1
n	94	82	137	70
Ovulation rate	1.11	1.37	2.26	1.96
Fertility	.89	.85	.90	.87
Litter size at birth	1.11	1.16	2.00	1.68
Litter size 3 and more (%)	0	1	28	0
Litter size at 70 days	.99	1.05	1.74	1.59
Birth weight (Kg)	4.2	4.2	3.1	3.7
Body weight at 70 days (Kg)	21.1	20.4	18.7	19.9
Weight of lamb at 70 days /ewe lambing	20.9	21.9	32.5	31.6
Weight of lamb at 70 days /ewe mated	18.6	18.6	29.3	27.2

### PROSPECTS FOR THE IMPROVEMENT OF LITTER SIZE

Ovulation rate (OR) and embryo survival (ES) are the main components of prolificacy. All methods reviewed for increasing prolificacy act mainly on OR. Thus in the Lacaune meat breed, ewe lambs OR (2.24) is much higher than in the dairy strain (1.72), whereas when selection for increasing litter size started 15 years ago, prolificacy of these strains were similar.

OR can be recorded several times during the same breeding season and presents higher heritability than LS. OR being the limiting factor of LS for low prolific breeds, a selection on this criterion should result in a LS increase. In the Mérinos d'Arles breed, (LS=1.11) the introgression of the Booroola Fec gene provides a good example of this change (Mérinos F+, LS=2.00). However, the ES declines when the number of embryo increases (Hanrahan and Piper, 1982). Thus, for prolific breeds there is an optimum OR which maximises LS. This optimum varies according to the breed (5 in Romanov, 3 in Lacaune). Even at non optimum value of OR, increasing ES is of interest. Embryo mortality induces a low birth weight of surviving embryos and consequently a poor peri-natal viability (Kelly and Johnstone, 1982). For instance, in the Romanov breed, lambs born as twins from double ovulations are 210 g heavier than lambs from higher OR and their viability is 96% versus 89% (Lajous, 1987).

Embryo losses are largely dependent on the number of ovulations, and breeds or strains have to be compared after adjustment for phenotypic effect of OR. The most appropriate method for adjusting for such effect is not clear. Until recently, the breed variability of ES was much debated, but there is no doubt now that such a variability exists (Bodin *et al.*, 1992). The importance of permanent differences among ewes (phenotypic or/and genetic) is poorly documented. Hanrahan (1982) reported low estimates of repeatability for ES adjusted for OR effects (0.07 ±0.04). The repeatability of ES in Romanov was estimated at 0.04 by Ricordeau *et al.* (1986) and recently confirmed with a phenotypic correlations between ES at the first and second pregnancy of 0.02. Estimations of  $h^2$  of ES are scarce, generally low ( $h^2 < 0.05$ ), and had poor accuracy due to the difficulties of estimation of this all or none trait. Animal model estimations on data from an experimental Romanov flock, provided heritabilities of ES below 0.04 at first and second pregnancy while  $h^2$  of OR was 0.16 and 0.27 at the same ages. Globally a sensible conclusion could be that genetic variation makes only a minor contribution to observed within-population differences in embryo survival considered as a dam trait. However, large differences observed on trophoblastin secretion by embryos of two groups of dams differing widely on their ES breeding value, showed that other within-breed genetic variability might exist (Bodin *et al.* 1994). Direct and indirect responses in several selection experiments

allow to conclude that embryo survival and ovulation rate are genetically independent in sheep, (Hanrahan and Quirke, 1985 ; Schoenian and Burfening, 1990 ; Hanrahan, 1990).

Mean LS was successfully increased in populations where selection, crossbreeding and/or major genes introgression were organised. In some cases that increase was even too high considering for instance some of the Booroola carrier populations, some first crosses with Finn, or the French Lacaune population where lambs born as triplets or more, represent 38% of lambs. Optimum prolificacy depends on the management, environment and economic situation, birth weights, viability and growing rates of lambs decreasing in multiple births. Moreover the artificial rearing required for high litter size increases production costs. In most situations, the higher profit of meat sheep farming is achieved with dams which lamb twins. Limitations on high LS or homogenization of prolificacy is a new challenge, in particular in harsh conditions where an unstable environment induces large variability of litter size.

A genetic variability of litter size homogeneity exists, some breeds being less variable than other breeds. Comparisons are significant only if the mean prolificacy is similar. For instance, the Spælsau Norwegian breed displays a very low variability ( $\mu=1.93$  ;  $CV=0.26$  ; %LS1=16.9 , %LS2=73.5 , %LS3=9.6) compared to the similar prolific French Lacaune breed ( $\mu=1.93$  ;  $CV=0.41$  ; %LS1=32.2 , %LS2=44.1 , %LS3=22.2 , %LS4=2.0). Within breed, this variability may also be proven.

As shown in laboratory species (Kaufman *et al*, 1977), the underlying genetic control of the ability to maintain a given level of performance is a complex phenomenon which may be related to different sources : heterozygosity at the QTLs controlling the traits, sensitivity of inbred individuals to changing environment and modifier genes. In a first approach, increasing the proportion of twin lambings, might be considered as a possible breeding objective. This trait fits the breeder demands and is heritable, even if poorly as shown table 7.

**Table 7** Heritability of LS and percent of twin lambings in the Lacaune breed.

Trait	N of data	N of sires	$h^2$ (GFcat)	$h^2$ (Mivque0)
LS	7377	109	0.27	0.22
%LS = 2	7377	109	0.13	0.08

The statistical problems of estimating the genetic part of the residual variance of such a categorical trait, the experimental designs for a best expression of individual ability and the risk of a too rapid decrease of the genetic variability have to be considered in order to achieve an intelligent design of breeding plans.

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