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Selection for prolificacy: New prospects for an ever-interesting objective

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SUMMARY – Selection for prolificacy is of major economic interest in most husbandry situations. However, there is an optimum litter size for each environment which maximizes the return profit per ewe. Uniform optimum litter sizes result in the highest profit, and when mean prolificacy of a breed is close to this optimum, then uniformity of litter sizes is a new additional objective. Genetic models involving genes controlling the mean as well as its environmental variability have been developed and used with data on the Lacaune breed. A genetic component for uniformity of litter size has been found, showing that selection for decreasing variability of prolificacy would be possible.

Key words: Canalising selection, economic optimum, prolificacy, sheep.

RESUME – *"Sélection pour la prolificité : De nouvelles perspectives pour un objectif toujours intéressant". La sélection pour la prolificité a un intérêt économique important dans la plupart des situations d'élevage. Cependant, dans chaque milieu il y a une taille optimale de portée qui maximise la rémunération par brebis. En raison de cet optimum, des tailles optimales uniformes de portée donnent le bénéfice le plus grand ; et lorsque la prolificité moyenne d'une race est près de cet optimum, l'uniformité des tailles des portées est un nouvel objectif additionnel. Les modèles génétiques impliquant des gènes contrôlant la moyenne ainsi que leur variabilité environnementale ont été utilisés et développés avec des données sur la race Lacaune. Une composante génétique pour l'uniformité de la taille de la portée a été trouvée, conduisant à prédire que la sélection pour la variabilité décroissante de la prolificité peut être possible.*

Mots-clés : *Canalisation de la sélection, optimum économique, prolificité, ovin.*

Conception rate (prolificacy) stands among the main objectives of most selection schemes of suckling ewes. Indeed, the size of the litter at birth is an essential component of the productivity of animal husbandry, which contributes more to the variability of weight in lambs weaned by the ewe than the individual growth of lambs. Genetic improvement of prolificacy may be obtained by crossing a local breed with a prolific breed, by the use of a synthetic breed obtained, by selection in pure breed, or introgression of a major gene. There is an optimum strategy for each type of environment (fodder resources, types of animal husbandry, local breed ability, etc.).

This economic interest of prolificacy has clearly been highlighted by several authors, and more recently by M. Benoit (pers. comm.), who has compared the gross marginal rates (excluding structural charges) and the profits (including structural charges) of ewes lambing 1, 2 or 3 lambs from data registered for a hardy breed and an improved breed (Table 1). Bearing in mind that multiple lamb growth is slightly inferior to that of single lambs, and that their death rate is slightly superior, the gross marginal rate of 2- or 3-lamb litters is not twice or three times higher than the gross marginal rate for single lambs, but, it is quite close. According to expectations, the relative increase of profits from ewes regarding their prolificacy is more important for the hardy breed than for the improved one, for which depreciation of the "quality" of multiple-born lambs is relatively higher (Table 1). In both cases of analysis (traditional semi-extensive husbandry of a hardy breed of the centre of France and a breed for meat in semi-intensive conditions), this economic interest of the litters of triplets can be observed. The lack of litters of quadruplets does not allow for measuring the profit of such a prolificacy. However, the mortality of multiple lambs which is very high, the need to recur to artificial lactation, the lengthening of the fattening period for lambs with poorer weight at birth can allegedly cause a drastic decrease of profit per ewe within litters of 4 or more.

Table 1. Economic interest of litter size (LS) (see text)

Litter size	1	2	3
Hardy breed			
Gross margin/ewe (FF)	326	665	843
Profit/ewe (FF)	76	415	593
Relative profit/ewe	100	546	780
Proven breed			
Gross margin/ewe (FF)	413	793	982
Profit/ewe (FF)	124	503	692
Relative profit/ewe	100	405	558

Thus, there is an optimal litter size which maximizes the benefit rate, but which varies according to the breed and production system. For the Lacaune breed, the rise in prolificacy provided by selection has led to the appearance of lambing for which the size of litter is higher than the economical optimum (Table 2). The average prolificacy of the daughters of elite sires mated to ram's mothers is nowadays much higher than the demands of breeders who have since largely modified their selection practice. As Bradford already pointed out in 1985, an additional objective to prolificacy, which is valid for all production systems, is the uniformity of litter sizes around the optimum desired. Variability among breeds as regards uniformity of litter size is already well-known (Bradford, 1985; Torstein, 1985; Bodin and Elsen, 1989, Fig. 1). When Bradford compares the weaned lambs' weight within two flocks (Spaelsam and Barbados) with an identical mean prolificacy (prol. = 1.95) but a different variability, he finds a superiority of near 10% for the flock with a lower variability. In Benoit's economical study (above mentioned), a superiority of about 24% appears within both breeds for ewes lambing twins twice in succession over those lambing triplets and latter a single lamb (Table 3).

Table 2. Change with time of the LS distribution (natural oestrus) of adult ewes in the Lacaune selection nucleus

	LS							
	1	2	3	4	5	6	7	Mean
Year 1988	45.8	46.5	6.6	1.0	0.2			1.63
Year 1996	34.7	47.7	13.6	3.3	0.5	0.1	0.02	1.88

Table 3. Economic interest of canalization. Comparison of profit from ewes with 2 lambings of twins and ewes lambing once a single lamb and once triplets

	Canalized	Variable	Relative profit
	LS 2+2	LS 1+3	% (C-V)/V
Hardy breed			
Gross margin/ewe (FF)	1330	1169	+13.8
Profit (FF)	830	669	+24.0
Proven breed			
Gross margin/ewe (FF)	1586	1395	+13.7
Profit (FF)	1066	816	+23.3

The capacity of maintaining a constant level of production is a complex phenomenon, which can have different genetic origins such as heterozygocy of certain genes controlling the trait or the existence of modifying genes which increase the phenotype stability. This hypothesis of the mean and variability of a trait being determined by different genes has led to propose a genetic modelling of canalisation.

The model proposed by SanCristobal-Gaudy *et al.* (1998) corresponds to the modelling of Rendel and Sheldon's observations (1960). They show that the canalising selection orientates indeed the mean population towards an optimum and the residual variance is reduced. Thus, some individuals seem less sensitive than others to environment variations, this particularity being under genetic control, since it responds to selection.

Like Wagner *et al.* (1997) propose, the effect of a locus on the residual variance could be explained by a multiplying factor of this variance linked to the locus. This model can be extended to a polygenic or infinitesimal model. These models are also perfectly justified for categorical traits such as litter size, if we previously consider the existence of an underlying variable distributed normally, and a set of parameters defining the class of observation.

The possibilities of canalising litter size have been explored for Lacaune breed. The data regarded 11 723 first litters of daughters of 157 sires on progeny test throughout 10 years of selection within 57 flocks. The model used come from successive changes of the classic model (Table 4). It considers that an individual's phenotype is a function of two genetic values, which contribute to the mean and the environmental variance. It has allowed to see clearly the main sources of heterogeneity for litter size variability. The genetic effect contributes significantly to the variability of distribution, unlike all the other effects tested, i.e. age, lambing season or flock. Table 5 shows the differences in expected distribution of litter size for daughters of sires of identical prolificacy mean values. This same analysis allowed us to calculate the sire component of the variance over the mean and over the log of the residual variance (SanCristobal-Gaudy *et al.*, 2000).

Table 4. Changes of the classical prediction model of conditional distribution of y/U leading to the canalization model

Classical model		μ_{ijklm}	=	$\beta_{ijkl} + u_m$
		σ^2_{ijkl}	=	σ^2_e
	=			
		μ_{ijklm}	=	$\beta_{ijkl} + u_m$
		$\log \sigma^2_{ijkl}$	=	$\log \sigma^2_e = \eta$
Heteroscedastic model		μ_{ijklm}	=	$\beta_{ijkl} + u_m$
		$\log \sigma^2_{ijkl}$	=	$\eta + \delta_{ijkl}$
Canalization model		μ_{ijklm}	=	$\beta_{ijkl} + u_m$
		$\log \sigma^2_{ijklm}$	=	$\eta + \delta_{ijkl} + \square_m$

Table 5. Expected distribution of litter size for daughters of Lacaune sires of identical mean prolificacy

	LS					Prolificacy
	1	2	3	4	N	
Sire A	34	52	12	2	345	1.94
Sire B	43	39	13	5	195	1.90

The environmental variance of litter size for Lacaune breed shows a heterogeneity due partially to an additive genetic factor which has been estimated. That shows that it is possible to achieve selection for an optimum mean value by reducing variability. However, the relative significance of each variable (mean and variance) depends on the situation for each generation. In order to meet a common final objective, there are many different procedures to follow (combination of weights for mean and variance for each generation). In particular, there is a faster way and a more profitable way different from that whose objective is constant for each generation. Research on how to optimise the relative weight of mean and variance throughout generations is currently being done.

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