

Genetic improvement of litter size in sheep. A comparison of selection methods

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(Received 22 February 1994; accepted 1 August 1994)

Summary – The objectives of this work were to examine the usefulness of measuring ovulation rate (OR) in order to improve genetic progress of litter size (LS) in sheep and to study different selection criteria combining OR and prenatal survival (ES) performance. Responses to selection for 5 generations within a population of 20 male and 600 female parents were compared using Monte-Carlo simulation techniques with 50 replicates per selection method. Two breeds with low (Merino) and medium (Lacaune) prolificacy were considered. Records were generated according to a bivariate threshold model for OR and ES. Heritabilities of OR and ES in the underlying scale were assumed constant over breeds and equal to 0.35 and 0.11, respectively, with a genetic correlation of -0.40 between these traits. Four methods of genetic evaluation were compared: univariate best linear unbiased prediction (BLUP) using LS records only (b-LS); univariate BLUP on OR records (b-OR); bivariate BLUP using OR and LS records (b-ORLS); and a maximum *a posteriori* predictor of a generalised linear model whereby OR was analysed as a continuous trait and ES as a binary threshold trait (t-ORES). Response in LS was very similar with b-LS, b-ORLS and t-ORES, whereas it was significantly lower with b-OR. Response in OR was maximum with b-OR and minimum with b-LS. In contrast, response in ES was maximum with b-LS. This study raised the question as to why selection based on indices combining information from both OR and ES did not perform better than selection using LS only.

litter size / ovulation rate / prenatal survival / sheep / threshold model

Résumé – Amélioration génétique de la taille de portée chez les ovins. Comparaison de méthodes de sélection. Cet article discute l'intérêt du taux d'ovulation (OR) pour accroître le progrès génétique sur la taille de portée (LS) et étudie à cet effet divers critères de sélection combinant OR et le taux de survie embryonnaire (ES). On a examiné par simulation les réponses à la sélection en 5 générations dans une population de 20 et 600 reproducteurs mâles et femelles avec 50 répliquations par méthode. On a considéré 2 races, de prolificité faible (Mérinos) et moyenne (Lacaune). Les performances ont été générées à partir d'un modèle bicaractère à seuils. Les héritabilités d'OR et ES ont été supposées constantes sur l'échelle sous-jacente dans les 2 races et prises égales respectivement à 0,35 et 0,11 avec une corrélation génétique entre ces 2 caractères de $-0,40$. Quatre méthodes d'évaluation génétiques ont été comparées : i) Blup unicaractère basé sur LS (b-LS) ; ii) Blup unicaractère basé sur OR (b-OR) ; iii) Blup bicaractère basé sur OR et LS (b-ORLS) ; iv) Prédicteur du maximum a posteriori bicaractère d'un modèle linéaire généralisé où OR est traité comme un caractère continu et ES comme un caractère à seuils (t-ORES). Les réponses observées étaient très voisines avec b-LS, b-ORLS et t-ORES, alors que b-OR donne une réponse significativement inférieure. La réponse sur OR était maximum avec b-OR et minimum avec b-LS, tandis que la réponse sur ES était maximum avec b-LS. Cette étude pose la question de savoir pourquoi la sélection basée sur des indices combinant OR et ES ne donne pas de résultats significativement supérieurs à la sélection sur LS.

modèle à seuils / ovins / prolificité / survie prénatale / taux d'ovulation

INTRODUCTION

Several studies support the conclusion that increased reproductive performance will improve economic efficiency of sheep breeding schemes (Nitter, 1987). Litter size (LS) is the trait receiving highest relative economic value in the Norwegian scheme (Olesen *et al*, submitted); the British Meat and Livestock Commission (1987) includes ewe reproduction performance in the selection indices in all except terminal sire breeds; selection schemes to improve LS are implemented in most breeds in France. Recommended economic indices used in the Australian Merino should result in substantial gain in number of lambs weaned, according to theoretical studies of Ponzoni (1986).

Litter size in sheep has been increased by direct selection (Hanrahan, 1990; Schoenian and Burfening, 1990) but the gains have not been very large because of the low heritability of LS. The average figure reported in the literature is 0.10 (Bradford, 1985). The categorical nature of this trait together with a possible physical upper limit (uterine capacity) may also have hindered genetic progress. Ovulation rate (OR) is considered to be the principal factor limiting litter size in sheep (Hanrahan, 1982; Bradford, 1985). Heritabilities of OR are typically larger than those of LS in most species, including sheep. Further, correlation between OR and LS is high and there is a nearly linear relationship with LS at ovulation rates up to 4 (*ie* Dodds *et al*, 1991). These results led Hanrahan (1980) to propose OR as an indirect criterion to select for LS. Before routine evaluation of OR is implemented, however, its advantage as selection criterion has to be assessed experimentally. Ovulation rate responded quite successfully to selection in Finnsheep (Hanrahan,

1992) and in Romanov (Lajous *et al*, quoted in Bodin *et al*, 1992) but, despite theoretical expectations, most of response in OR did not result in an increase of LS. The same phenomenon has been observed in mice (Bradford, 1969). In pigs, OR was increased by selection but correlated response in LS was smaller than expected (Cunningham *et al*, 1979).

A second possible criterion of selection is an index that combines OR and prenatal survival (ES). Johnson *et al* (1984) derived a linear index of OR and ES and they predicted that response using the index would be about 50% larger than with conventional direct selection on LS in pigs. Similar predictions are given by Bodin *et al* (1992) in sheep. However, selection experiments have not confirmed the expected advantage of an index for LS components, in mice (Gion *et al*, 1990; Kirby and Nielsen, 1993) or in pigs (Neal *et al*, 1989), whereas there is no experimental evidence in sheep yet. In all species, the apparent reason why OR or an index was no better criterion than LS was a correlated decrease in ES.

Cited predictions of response are implicitly based on an infinitesimal model with a continuous normally distributed trait. This model can be justified for OR in pigs or mice but certainly not for ES, which is a dichotomous trait. Pérez-Enciso *et al* (1994a) examined the implications of generating OR and ES records according to a bivariate threshold model. In this model, 2 underlying (unobserved) normal variates which are negatively correlated and a set of fixed thresholds are assumed. The main implications of a bivariate threshold model for litter size components are: (i) the existence of a non-linear antagonistic relationship between OR and ES, *ie* correlation between LS and OR decreases as OR augments; (ii) as a consequence, a linear index combining OR and ES, which gives a constant weight to ES over all the range of OR, is not the optimum selection criterion to increase LS in all generations; and (iii) litter size behaves as a natural index close to the optimum selection criterion combining OR and ES, at least in the situation analysed (mass selection and equal information on candidates). Points (ii) and (iii) are especially relevant because the theory based on a linearisation of the model predicted an advantage of the index over LS, which was not fully achieved in the simulation. This is precisely the situation encountered in selection experiments, where a linear index of OR and ES has not proved to be significantly better than direct selection on LS (see review of Blasco *et al*, 1993) regardless of optimistic predictions.

The objectives of this work were: (i) to examine in a more realistic situation than in a previous report (Pérez-Enciso *et al*, 1994a) the usefulness of measuring OR in order to improve genetic progress of LS in sheep using overlapping generations and all family information; and (ii) to study different selection criteria combining OR and ES performances. The influence of genetic correlation between OR and ES has also been considered. Work was carried out using stochastic computer simulation. Records were generated according to a bivariate threshold model. Two breeds with low and medium prolificacy, Merino and Lacaune, respectively, were considered.

MATERIALS AND METHODS

Selection scheme

A population of 600 dams and 20 sires was simulated. After each breeding season, when new records from OR and LS were available, old and newborn animals were evaluated according to 1 of several methods described below. The worst 120 dams (20%) and the worst 10 sires (50%) were discarded and replaced by the best 120 newborn females and the best 10 newborn males. Only 1 female and 1 male offspring per dam per breeding season were allowed and the maximum number of male offspring to be selected from each sire was set to 3. A control line was simulated where sires and dams were chosen at random. Results were expressed as deviations from the control line, in order to correct for the effect assigned to each breeding season. Five cycles of selection were simulated and 50 replicates for each selection method were run.

Two populations were considered, a low prolific breed (Merino) and a more prolific breed (Lacaune). Phenotypic means and variances are shown in table I for nulliparous and non-nulliparous ewes of both breeds. These figures are based on performances in INRA experimental herds for Merino and on-farm recording for Lacaune. Ovulation rate and LS increased with parity order even if prenatal survival was lower. Phenotypic correlations between OR and ES were -0.56 and -0.38 in Merino and Lacaune, respectively. Note that populations with higher means had higher variances but that coefficient of variation remained approximately constant, as commonly observed (Nitter, 1987).

Table I. Phenotypic means and variances for first and following parities of ovulation rate (OR), prenatal survival (ES) and litter size (LS).

<i>Trait</i>	<i>Parity</i>	<i>Breed</i>			
		<i>Merino</i>		<i>Lacaune</i>	
		<i>1</i>	<i>>1</i>	<i>1</i>	<i>>1</i>
OR	Mean	1.50	1.75	2.29	3.05
	Variance	0.545	0.567	0.762	0.880
ES	Mean	0.83	0.76	0.83	0.70
	Variance	0.141	0.182	0.141	0.210
LS	Mean	1.24	1.33	1.91	2.15
	Variance	0.441	0.543	0.942	1.020

Generation of records

Records of OR, ES and LS were generated as described in detail in Pérez-Enciso *et al* (1994a). In short, both OR and ES were categorical variates assumed to be determined by a threshold liability process with normally distributed underlying variables. For a given ovulation rate, ES was simulated drawing random numbers

from a Bernoulli distribution with appropriate parameters. Litter size was the number of embryos surviving. Thresholds were set to match observed frequencies in each category of OR and ES. Heritabilities of OR and ES in the underlying scale were 0.35 and 0.11, respectively, in both breeds. Repeatabilities of OR and ES were 0.70 and 0.22, respectively. Genetic correlation between OR and ES was -0.40 in both breeds. Environmental correlations were -0.32 and -0.22 in Merino and Lacaune, respectively. Given that there exists uncertainty about the genetic parameters, especially for genetic correlation between OR and ES, other correlations were considered in the Lacaune breed. The model used to simulate records included animal plus common environment as random effects. Fixed effects were parity, with 2 levels, first and following parities, and year, with 5 levels. Values for the effect of parity in the underlying scale were chosen as to match figures in table I. The effect of year was simulated such that maximum differences between the 'best' and 'worst' years were about 10% in LS.

Genetic evaluation

Four methods of genetic evaluation were compared: 1) univariate BLUP using LS records only (b-LS); 2) univariate BLUP on OR records (b-OR); 3) bivariate BLUP using OR and LS records (b-ORLS); and 4) a bivariate non-linear model whereby OR was analysed as a continuous trait and ES as a binary threshold trait (t-ORES; Foulley *et al*, 1983). Here equations derived by Janss and Foulley (1993) were adapted to take into account that for each record of the 'continuous' trait (OR), there were as many observations of the binary trait (ES) as number of ova shed (see *Appendix*). The original program (LLG Janss, personal communication) was optimised to solve the system of equations by sparse matrix methods using FSPAK (Pérez-Enciso *et al*, 1994b). In agreement with the simulation, the statistical model in all methods included parity and year as fixed effects, and animal and permanent environmental effect as random effects. Criterion b-LS is that currently implemented where sheep are evaluated for their reproductive performance (Bolet and Bodin, 1992; Olesen *et al*, submitted), whereas b-OR responds to Hanrahan's (1980) suggestion of using OR as indirect criterion to select for LS. Finally, b-ORLS and t-ORES are different ways of combining OR and ES performance. In b-ORLS, a direct estimation of the breeding values for LS is obtained, whereas in t-ORES the estimated breeding values of OR and ES have to be combined in an index for LS. The index chosen was that suggested by Wilton *et al* (1968), *i.e.* for the *i*th animal,

$$I_i = \hat{y}_{OR_i} \hat{y}_{ES_i} \quad [1]$$

where \hat{y}_{OR_i} , the predicted ovulation performance, is

$$\hat{y}_{OR_i} = \hat{h}_{OR_1} + \hat{p}_{OR_1} + \hat{a}_{OR_i} + \hat{c}_{OR_i} \quad [2]$$

where \hat{h}_{OR_1} and \hat{p}_{OR_1} are estimations (maximum *a posteriori*, MAP) of first year and first parity obtained by solving the t-ORES equations and, similarly, \hat{a}_{OR_i} and \hat{c}_{OR_i} are predictions (MAPs) of *i*th breeding value and *i*th permanent environmental

effect, respectively. In [1], the predicted ES probability is

$$\hat{y}_{ES_i} = \Phi \left(\hat{h}_{ES_1} + \hat{p}_{ES_1} + \hat{a}_{ES_i} + \hat{c}_{ES_i} \right) \quad [3]$$

In equation [3], \hat{h}_{ES_1} , \hat{p}_{ES_1} , \hat{a}_{ES_i} and \hat{c}_{ES_i} are MAPs obtained from solving the t-ORES equations. Note that because [1] is a nonlinear index genetic merit depends on levels of fixed effects. The index was chosen to maximise response in first parity. Alternatively, a weighted average of all parities could also have been applied (Foulley and Manfredi, 1991).

Methods were evaluated in terms of elicited response to selection but goodness of fit, as suggested by Pérez-Enciso *et al* (1993), was also studied. Correlations between observed and fitted records were computed. For b-LS and b-ORLS methods, fitted LS records of i th animal in the j th year and k th parity were obtained from

$$\hat{y}_{LS_{i,j,k}} = \hat{h}_{LS_j} + \hat{p}_{LS_k} + \hat{a}_{LS_i} + \hat{c}_{LS_i}$$

where \hat{h}_{LS_j} , \hat{p}_{LS_k} , \hat{a}_{LS_i} , and \hat{c}_{LS_i} are best linear unbiased estimate (BLUE) and BLUP solutions to fixed and random effects obtained for the LS location parameters. In the case of t-ORES, fitted LS records were computed from an expression similar to [1] except that corresponding year and parity solutions were used. Ovulation records were fitted from expressions similar to [2] and ES records from expressions similar to [3].

Note that OR was treated in all cases as a continuous variate even though it was simulated following a threshold model. There is evidence, nonetheless, that the advantage of a threshold model over a linear model for genetic evaluation diminishes very quickly for more than 1 threshold (Meijering and Gianola, 1985).

Genetic variances used for genetic evaluation were those in the observed scale, except for ES in t-ORES. They were obtained by simulation from the definition of breeding value in the observed scale, *ie* mean phenotypic value conditional on genotype. Heritabilities of LS were 0.14 and 0.15, and 0.23 and 0.30 for OR in Merino and Lacaune, respectively. The heritability of ES was 0.06 in both breeds. Genetic correlation between LS and OR was 0.83 and between LS and ES, 0.17.

RESULTS

Selection responses for LS in the first generation are shown in tables II and III for Merino and Lacaune, respectively. An increase in LS of about 5–6% of the mean was achieved in both breeds. Changes were relatively more important in first than successive parities. Response in LS was very similar whether selection was directly on LS or using OR as indirect selection criterion. Considering information on both OR and LS (or equivalently OR and ES) produced only a small increase in response with respect to direct selection on LS. Performance of b-ORLS and t-ORES was almost identical. Even if index [1] was derived to maximise response in first parity, correlated response in successive parities was as high as with linear methods, *ie* b-ORLS, in which weights do not depend on location parameters. This suggests that, from a practical viewpoint, the nonlinear index proposed by Foulley

Table II. Mean response in first generation of selection for litter size (ΔLS), ovulation rate (ΔOR) and embryo survival (ΔES) in Merino.

<i>Method</i>	ΔLS_1	$\Delta LS_{>1}$	ΔOR_1	$\Delta OR_{>1}$	ΔES_1	$\Delta ES_{>1}$
b-LS	0.08	0.06	0.10	0.04	0.003	0.017
b-OR	0.07	0.07	0.14	0.11	-0.023	-0.008
b-ORLS	0.10	0.08	0.13	0.11	-0.003	-0.006
t-ORES	0.10	0.07	0.13	0.12	-0.006	-0.007

Subindices refer to first (1) and following parities (> 1). Maximum empirical standard errors were 0.02 for ΔLS and ΔOR and 0.004 for ΔES .

Table III. Mean response in first generation of selection for litter size (ΔLS), ovulation rate (ΔOR) and embryo survival (ΔES) in Lacaune.

<i>Method</i>	ΔLS_1	$\Delta LS_{>1}$	ΔOR_1	$\Delta OR_{>1}$	ΔES_1	$\Delta ES_{>1}$
b-LS	0.11	0.12	0.12	0.06	0.005	0.025
b-OR	0.11	0.11	0.18	0.20	-0.018	-0.012
b-ORLS	0.14	0.13	0.16	0.19	0.005	-0.002
t-ORES	0.14	0.11	0.16	0.19	-0.001	-0.008

Subindices refer to first (1) and following parities (> 1). Maximum empirical standard errors were 0.02 for ΔLS and ΔOR and 0.004 for ΔES .

and Manfredi (1991, equation [62]), whereby predicted performance is weighted according to frequencies of the different subclasses, might be robust to different weights.

Changes in LS were relatively similar across selection methods but they were not for the components, OR and ES (tables II and III). Ovulation rate increased twice as much when selection was on OR than on LS. However, only about half of that increase corresponded to an increase in LS with b-OR ($\Delta LS/\Delta OR \approx 0.50$), whereas the ratio $\Delta LS/\Delta OR$ was always larger than 0.80 with b-LS. Methods b-ORLS and t-ORES induced changes in OR similar to b-OR. Correlated changes in ES were also different depending on the method of selection. Selection using b-LS was accompanied by an increase in prenatal survival of about 2%. All other methods, especially b-OR, resulted in lower ES.

Response of LS in the following generations is plotted in figure 1. Unlike results in tables II and III, it is evident that indirect selection on OR was the poorest method in the long term, especially in the more prolific breed, Lacaune. Direct selection on LS was only slightly worse than selection based on either b-ORLS or t-ORES. Responses were not significantly different among methods in any generation with the sole exception of b-OR. Figure 2 shows correlated changes in OR phenotype. As expected, b-OR caused the largest increase in OR and b-LS, the minimum. Methods b-ORLS and t-ORES behaved very similarly. Figure 3 shows qualitative differences between breeds with respect to the evolution of prenatal survival. Overall, ES in-

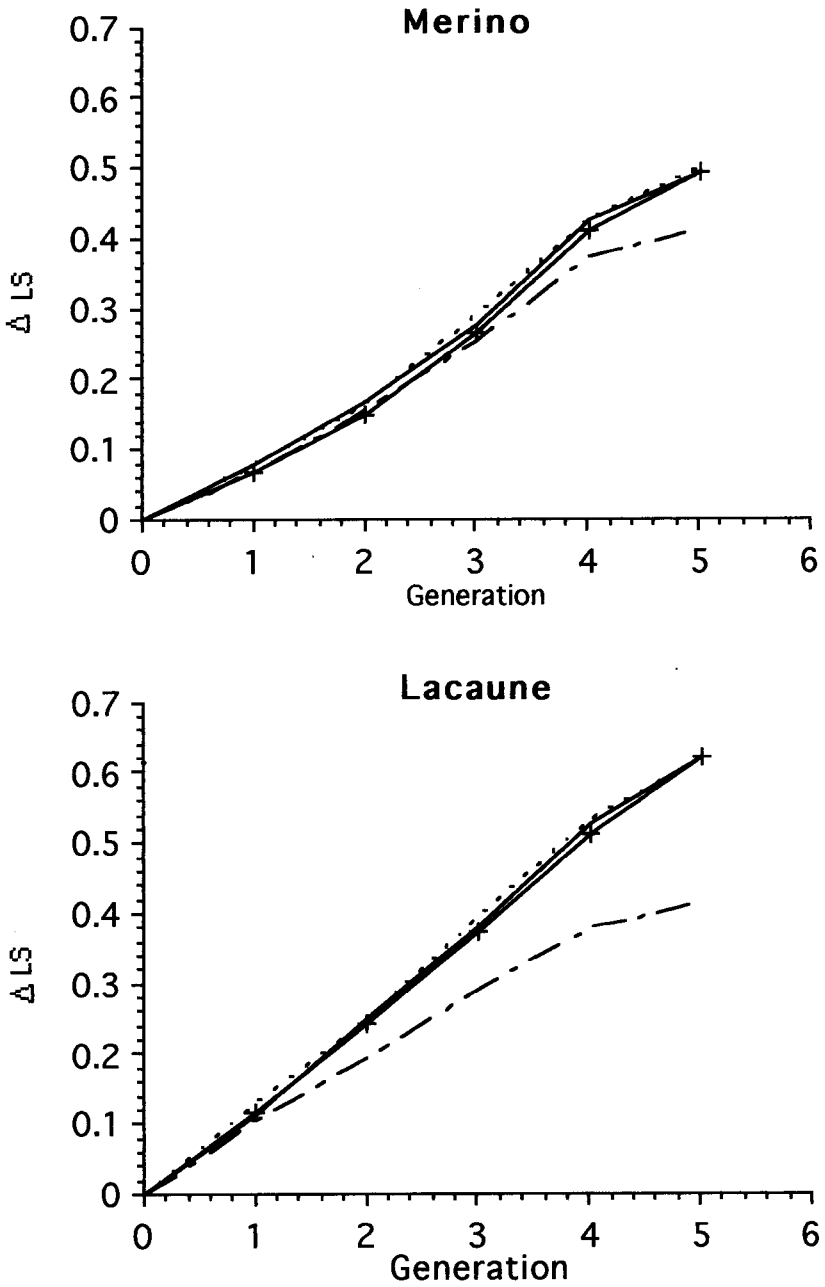


Fig 1. Mean response of litter size according to different methods: b-LS (+), b-OR (---), b-ORLS (···), and t-ORES (-·-·), in Merino and Lacaune; average of all parities.

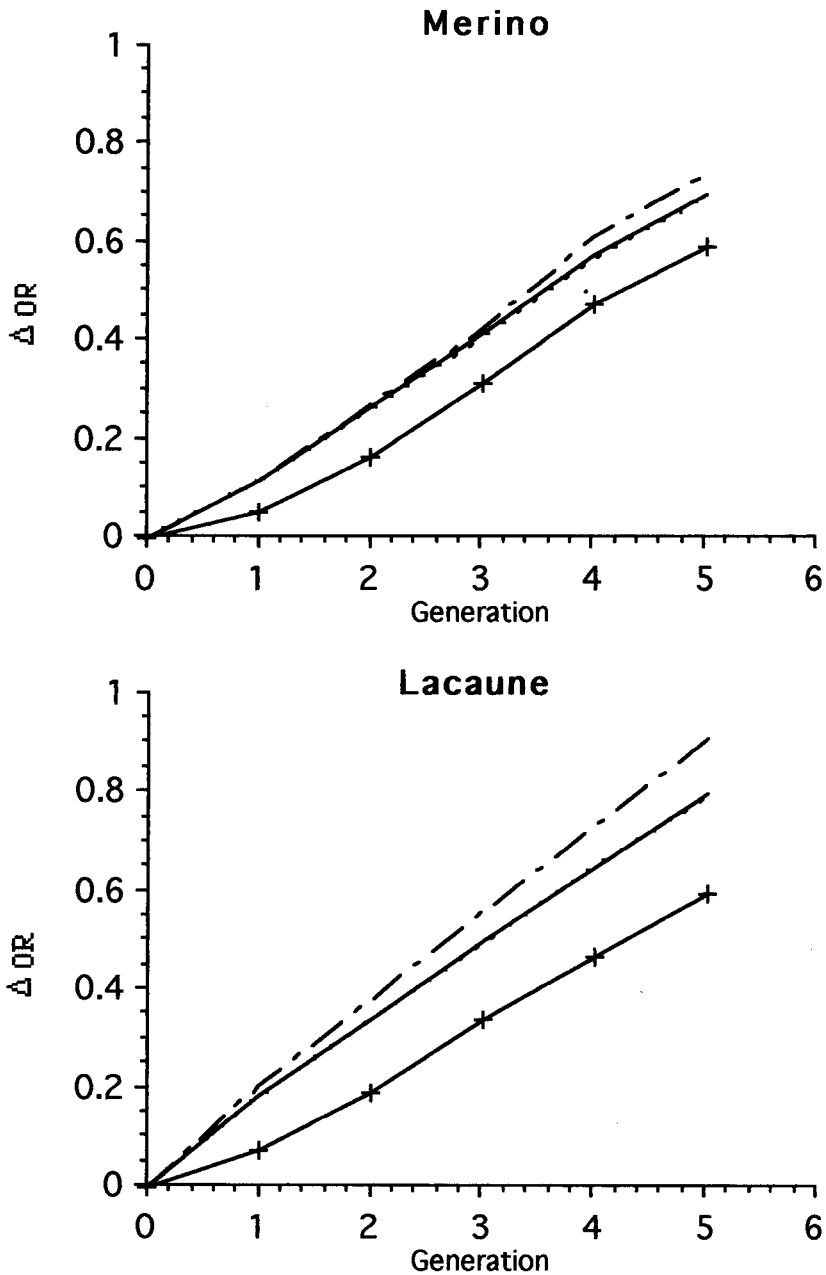


Fig 2. Mean response of ovulation rate according to different methods: b-LS (---+), b-OR (---), b-ORLS (···), and t-ORES (----), in Merino and Lacaune; average of all parities.

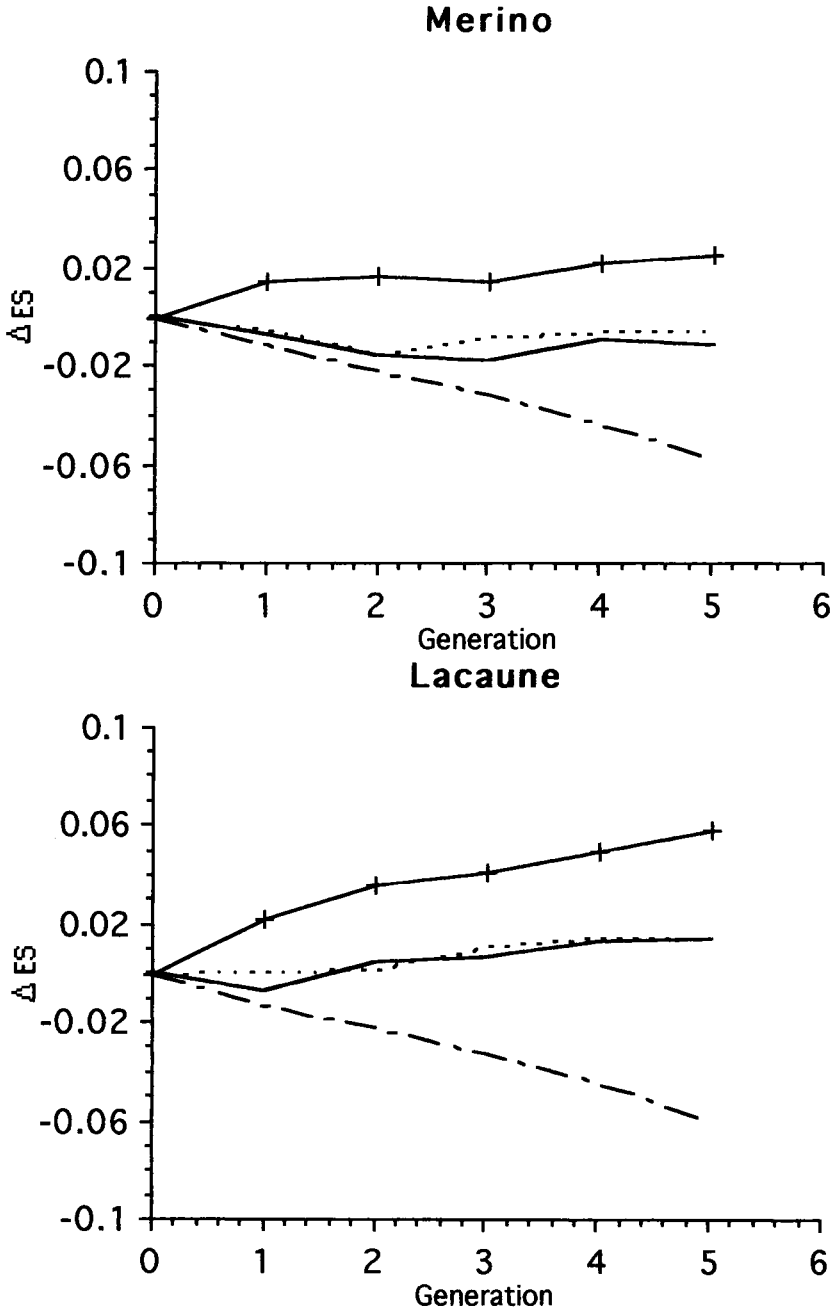


Fig 3. Mean response of prenatal survival according to different methods: b-LS (+—), b-OR (— — —), b-ORLS (· · ·), and t-ORES (— · — ·), in Merino and Lacaune; average of all parities.

creased more in Lacaune than in Merino. Direct selection for LS in Merino induced no correlated phenotypic change in ES (except in the first generation), whereas survival increased regularly in Lacaune. In Merino, phenotypic trends were negative with b-ORLS and t-ORES in the first 2 generations but ES remained constant or increased thereafter. This highlights that b-ORLS and t-ORES are nonlinear selection criteria with respect to underlying genotypes. Selection on OR induced a negative response in ES because of the negative genetic correlation between both traits.

Correlations between observed and fitted records are shown in table IV for the traits studied. All methods were very close to each other regarding the degree of fit within trait.

Table IV. Mean correlation between observed and fitted records of litter size (LS), ovulation rate (OR) and prenatal survival (ES).

<i>Trait</i>	<i>Method</i>	<i>Merino</i>	<i>Lacaune</i>
LS	b-LS	0.75	0.74
	b-ORLS	0.73	0.72
	t-ORES	0.71	0.73
OR	b-OR	0.83	0.86
	b-ORLS	0.84	0.86
	t-ORES	0.83	0.86
ES	t-ORES	0.61	0.69

Previous results assumed a genetic correlation between OR and ES ($\rho_{\text{GOR,ES}}$) of -0.4 . Consequences of using different values of the genetic correlation were examined in Lacaune. Table V shows how different parameters are affected by a change in $\rho_{\text{GOR,ES}}$. In all cases phenotypic correlation and heritabilities of OR and ES were constant, thus environmental correlation decreased as genetic correlation increased. Genetic correlations and heritabilities were obtained by simulation. Genetic correlation between LS and its components increased with $\rho_{\text{GOR,ES}}$, but the increase was much more noticeable between LS and ES than between LS and OR. In the extreme case of $\rho_{\text{GOR,ES}} = -0.9$, genetic correlation between LS and ES was less than zero. This negative genetic correlation was confirmed by a decrease in mean ES genotype when selection was performed on b-LS (results not shown). However, the ES phenotype did not change (table VI) perhaps because of the small decrease in the breeding value of ES. Heritability of LS decreased as $\rho_{\text{GOR,ES}}$ did. Thus a small heritability of LS could be due either to a low heritability of its components or to a highly negative genetic correlation between them (equation [11] in Pérez-Enciso *et al*, 1994a).

The effect of genetic correlation on response to selection is shown in table VI. Given the similar results between b-ORLS and t-ORES, only b-ORLS was studied, in addition to b-LS and b-OR. Method b-ORLS was chosen because of its lower computing cost and because genetic evaluations for LS are obtained directly without the need for an index. It can be seen that selection criteria became more similar as

Table V. Genetic parameters of litter size components as a function of genetic correlation between ovulation rate and embryo survival.

$\rho_{g_{OR,ES}}$	$\rho_{e_{OR,ES}}$	$\rho_{g_{OR,LS}}$	$\rho_{g_{ES,LS}}$	h^2_{LS}
-0.90	-0.08	0.83	-0.40	0.06
-0.40	-0.22	0.83	0.17	0.14
0.00	-0.33	0.87	0.47	0.21
0.40	-0.44	0.91	0.69	0.27

ρ_g , genetic correlation; ρ_e , environmental correlation; OR, ovulation rate; ES, prenatal survival; LS, litter size; h^2 , heritability in the observed scale; figures refer to Lacaune.

Table VI. Mean response in fifth generation for litter size in absolute terms (ΔLS) and relative to ovulation rate ($\Delta LS/\Delta OR$), and response in embryo survival (ΔES) for different values of genetic correlation between ovulation rate and embryo survival.

$\rho_{g_{OR,ES}}$	Method	ΔLS	$\Delta LS/\Delta OR$	ΔES
-0.90	b-LS	0.29	0.76	0.003
	b-ORLS	0.21	0.25	-0.102
	b-OR	0.10	0.12	-0.205
-0.40	b-LS	0.62	1.00	0.059
	b-ORLS	0.62	0.78	0.015
	b-OR	0.42	0.48	-0.059
0.00	b-LS	0.82	1.12	0.085
	b-ORLS	0.84	1.02	0.072
	b-OR	0.64	0.69	-0.004
0.40	b-LS	1.00	1.25	0.461
	b-ORLS	1.01	1.13	0.410
	b-OR	0.86	0.92	0.054

Figures refer to Lacaune.

genetic correlation increased. Methods b-LS and b-ORLS were not significantly different for moderate genetic correlations, whereas b-OR was consistently less efficient. The behaviour of the ratio $\Delta LS/\Delta OR$ depended strongly on genetic correlation. An increase in number of ova shed was followed closely by larger litter size for moderate correlations. However, as $\rho_{e_{OR,ES}}$ decreased so did $\Delta LS/\Delta OR$. Further, this ratio was always maximum with b-LS. Embryonic survival did not decrease with b-LS but did with b-ORLS when correlation was very low.

DISCUSSION

The results presented here are in agreement with simulation results reported previously (Pérez-Enciso *et al*, 1994a) where selection on OR or on an index combining OR and ES did not produce a significantly larger response than direct selection on LS. The slight advantage of b-ORLS and t-ORES over b-LS in the first breeding season did not persist over generations, due to a larger decrease in ES when information from OR was included in the selection criterion. Methods b-LS, b-ORLS and t-ORES behaved very similarly with respect to LS (fig 1), but differently with respect to OR and ES (fig 2 and 3). Oddly enough, including information from OR (a trait of moderate heritability and highly correlated with LS) did not result in a much higher response for LS but rather in a redistribution of weights given to OR and ES. Selection pressure on ES decreased in bivariate methods (b-ORLS and t-ORES) because correlation between OR and LS is much higher than that between ES and LS (table V). Phenotypic differences in ES among lines were small (about 3% between b-LS and b-ORLS in Lacaune) but it sufficed to compensate for different ovulation rates, a difference of approximately 0.2 ova between lines selected with b-LS and b-ORLS. In fact, one of the arguments adduced in favour of OR as indirect selection criterion is that phenotypic differences between control and selected lines were much larger in OR than in ES (Hanrahan, 1982). However, prenatal survival cannot be neglected even if its contribution to total variation of LS in the base population is small, in particular when genetic correlation between OR and ES is negative.

Using b-LS, increase in litter size corresponded exactly to the increase in OR for $\rho_{\text{GOR,ES}} = -0.4$ ($\Delta\text{LS}/\Delta\text{OR} = 1$ in table VI). This can be interpreted as if response to selection for LS were completely explained by a change in OR. In contrast, selection using OR produced a smaller response in LS with a much larger increase in OR ($\Delta\text{LS}/\Delta\text{OR} = 0.48$). This phenomenon was described by Bradford (1985) as “a striking example of asymmetrical correlated response” (underlining is ours). It is evident from results in table VI, however, that this apparent asymmetry is due to a different emphasis on ES in the two criteria. It is current opinion among sheep breeders that selection pressure on ES should become more important as mean OR increases. The results in table V highlight that this pressure also depends on the value of $\rho_{\text{GOR,ES}}$. As this correlation becomes more negative, selection pressure on OR relative to ES increases dramatically, especially if information on OR is used. Then, if prenatal mortality increases too much, as a result of a correlated change with OR, decline in ES will offset the increase in OR. For instance, for $\rho_{\text{GOR,ES}} = -0.9$ response in LS was slightly larger with b-ORLS than with b-LS in the first generation (results not shown) but the reverse was true in the fifth generation (table VI).

Matos (1993) reported correlations between fitted and observed LS records about 0.65 in Rambouillet and Finnsheep using linear models. These figures are relatively close to those reported here if we consider that in Matos' (1993) study variances had to be estimated from the same data set. In a similar study, Olesen *et al* (1994) reported lower correlations between fitted and observed LS records of Norwegian sheep, around 0.46, perhaps because the effects included in Matos' (1993) model were more realistic. Both studies also compared threshold and linear models in

terms of goodness of fit but the differences between methods were very small, in agreement with results in table IV.

The question whether LS can be increased more rapidly by using information on its components rather than by direct selection remains open. All experiments have failed in this respect (Blasco *et al*, 1993). A likely explanation is that indices combining OR and ES (or OR and LS) have not been optimum. Only linear indices with a constant weight to ES over all the range of OR have been tested experimentally, and these do not take into account the nonlinear phenotypic relationship among LS and its components. Pérez-Enciso *et al* (1994a) have shown that a separate index for each OR should be used. Nonlinear indices might overcome some of these handicaps. In this work, a simple nonlinear index (equation [1]) was examined. The exact equation is an integral that implies marginalization with respect to a large number of variables. The analytical solution to this integral is unknown. Equation [1] is a first-order approximation which will only be close to the optimal criterion if the amount of information on each individual is large (Gianola and Fernando, 1986). Results showed, however, that nonlinear indices (t-ORES) did not elicit a larger response in LS than linear indices (b-ORLS), perhaps because of the lack of information. Moreover genetic parameters in the observed scale are assumed to be constant but they depend on the population mean, which changes with selection. It should be recalled, nonetheless, that OR could be used as an early predictor for LS, given its high correlation with LS and its high repeatability. Measurement of OR would then allow us to decrease generation interval and increase the accuracy of genetic evaluation of young animals.

Certainly, the results presented here depend crucially on how likely a bivariate threshold model is, *ie* on the existence of 2 underlying continuous normal variates and a set of fixed threshold points. Because a statistical model is necessarily an oversimplification of reality, these conditions will never be met with strict rigour. There is, nonetheless, considerable literature on the plausibility and biological justification of the threshold model, see reviews by Curnow and Smith (1975) and Foulley and Manfredi (1991). With respect to reproductive traits, there is a complex interaction between continuous variates, *eg*, hormone levels, and discrete variates, *ie* number of ova and survival (Haresign, 1985). A threshold-like mechanism has been advocated to explain embryo mortality as a function of the degree of asynchrony between uterus and embryo (Wilmot *et al*, 1985).

In addition, covariation among LS components and selection experiment results can be used to check the validity of the threshold model. First, under the bivariate threshold model considered here, the phenotypic probability of embryonic survival at a given ovulation level is given by

$$\Phi \left[\frac{\mu_{ES} + b(x_{OR} - \mu_{OR})}{(1 - \rho^2)^{1/2}} \right] \quad [4]$$

(Pérez-Enciso *et al*, 1994a) where μ is the underlying mean, x is the underlying variable, b is the regression of x_{ES} on x_{OR} and ρ is the correlation between x_{ES} and x_{OR} . Equation [4] allows us to describe a decreasing correlation between OR and LS as OR increases, as commonly observed in real data (Hanrahan, 1982; Dodds *et al* 1990). Further, [4] can be written as $\Phi[\alpha + \beta(x_{OR} - \mu_{OR})]$ with $\beta = b/(1 - \rho^2)^{1/2}$. Now β can be estimated by 2 independent methods, either by probit regression of survival

on number of ova (Pérez-Enciso *et al*, 1994a), or from phenotypic covariances and variances (table I), assuming that [4] holds as well in the observed scale. With the parameters used here, values for β from the probit regression were -0.34 and -0.25 and, from phenotypic covariances, -0.37 and -0.18 for Merino and Lacaune, respectively. Agreement seems reasonable, especially for the less prolific breed.

Secondly, table V emphasises that genetic parameters for OR, ES and LS are interrelated. In particular, heritability of LS can be expressed, approximately, as

$$(\mu_{y_{OR}}^2 \text{Var}_{g_{ES}} + \mu_{y_{ES}}^2 \text{Var}_{g_{OR}} + 2\mu_{y_{OR}}\mu_{y_{ES}} \text{Cov}_{g_{OR,ES}}) / \text{Var}_{y_{LS}} \quad [5]$$

(Pérez-Enciso *et al*, 1994a), where μ_y is the phenotypic mean; $\text{Var}_g(\text{Cov}_g)$ the genetic variance (covariance) in the observed scale; and Var_y the phenotypic variance. It follows that for a given variability of OR and ES, heritability of LS is inversely related to genetic correlation between OR and ES. Thus given the phenotypic parameters in table I and provided heritabilities are moderate for OR and low for LS and ES, equation [5] allows us to predict a negative genetic correlation between LS components. Table VII shows how well [5] predicted heritabilities of LS in different studies reporting multivariate variance estimates of OR, LS and ES in pigs. Agreement between expected and estimated heritabilities was excellent in reported estimates in pigs. Note that Haley and Lee (1992) found no additive variation for ES and that in this case the smaller heritability of LS occurs due to the additional noise from embryonic mortality. A negative genetic correlation between OR and ES has also been evidenced by selecting on OR, which has been accompanied by a lower ES (Bradford, 1969; Cunningham *et al*, 1979; Hanrahan, 1992). Most reported estimates of genetic covariances between OR and ES in pigs and rabbits are also negative (Blasco *et al*, 1993). Furthermore, the magnitude of this correlation greatly influences the ratio of response in LS relative to OR ($R = \Delta\text{LS}/\Delta\text{OR}$). The more negative the genetic correlation, the bigger the difference in R between direct selection on LS and indirect selection on OR (table VI). There is experimental evidence supporting that the ratio R is larger for direct selection than indirect selection on OR as expected from results in table VI. For instance, R was 0.61 using direct selection in the Galway breed (Hanrahan, 1990), and 0.67 in Rambouillet (Schoenian and Burfening, 1990), whereas R was only 0.26 when Finnsheep were selected for OR (Hanrahan, 1992).

Table VII. Genetic relationships between litter size and its components in pigs.

Reference	n	h_{OR}^2	h_{ES}^2	$r_{g_{OR,ES}}$	h_{LS}^2	\hat{h}_{LS}^2
Bidanel <i>et al</i> (1992)	700	0.11	0.03	-0.13	0.11	0.12
Haley and Lee (1992)	382	0.30	0.00	0.00	0.09	0.08

n , number of records; h_{LS}^2 , expected heritability of litter size (from equation [5]); other abbreviations as in table V.

Finally, the most critical implication of this model refers to the relative advantage of direct selection for LS relative to other methods combining records of ES and OR.

Using mass selection, Pérez-Enciso *et al* (1994a) found in a simulation study that response in LS with an index combining OR and ES was similar to direct selection. Both methods were better than indirect selection on OR. In this study, where family information was used, the same conclusion applies. These results are compatible with experimental evidence in pigs and mice (Bradford, 1969; Cunningham *et al*, 1979; Neal *et al*, 1989; Gion *et al*, 1990; Kirby and Nielsen, 1993) where OR or an index combining OR and ES has not proved to be significantly better than direct selection on LS.

Several problems with the infinitesimal threshold model remain nonetheless. First, major genes affecting OR in sheep are known, the gene *Fec B* of the Booroola Merino being the best documented case. The presence of a major gene *per se* does not invalidate a threshold model, since it can be considered as a fixed effect that shifts the underlying mean, but it does change the dynamics of the population under selection. Thus predicted or simulated responses under an infinitesimal threshold model will be quite inaccurate. Genes with a significant effect on OR are also being identified in other species such as mice (Spearow *et al*, 1991) but evidence is conflicting in pigs (Mandonnet *et al*, 1992; Rathje *et al*, 1993). With respect to embryonic survival, a number of recessive genes that cause embryo lethality in mice have been identified (Rossant and Joyner, 1989). As information on effects and frequencies of QTLs affecting litter size accumulates, the implications of an infinitesimal threshold model should be reconsidered. The existence of major chromosomal abnormalities as a cause of embryonic mortality would also pose problems for the threshold model. In a recent review, Blasco *et al* (1993) quoted that lethal chromosome abnormalities are found in 5–10% of early pig and rabbit embryos, a non-negligible proportion. Deleterious reciprocal translocations and aneuploidies have been reported in sheep but the proportion of embryo deaths due to these abnormalities is uncertain (Bolet, 1986; Wilmut *et al*, 1986).

CONCLUSIONS

The main conclusions can be summarised as follows:

- (i) A bivariate threshold model can be justified based on statistical and experimental evidence.
- (ii) Ovulation rate was an effective criterion of selection for litter size in sheep only in the very short term. The advantage of using OR as an early predictor in order to decrease generation interval should be investigated.
- (iii) The ratio of response in litter size relative to ovulation rate ($\Delta\text{LS}/\Delta\text{OR}$) depends strongly on genetic correlation; the more negative the genetic correlation, the larger the difference in this ratio between direct selection for litter size and indirect selection on ovulation rate. Direct selection on litter size maximised the ratio $\Delta\text{LS}/\Delta\text{OR}$.
- (iv) Using information from both ovulation rate and embryonic survival was not significantly better than selection using litter size records exclusively. Selection with b-LS puts more pressure on survival than methods combining ovulation rate and embryonic survival, especially as genetic correlation decreased.

Several unresolved problems can be quoted:

- (i) The extent to which these conclusions apply to other situations and species such as mice, rabbits and pigs.
- (ii) The interpretation of breeding value for litter size and how to combine information from ovulation rate and prenatal survival in an optimal way.
- (iii) An analytical approach to predict response to selection with this model along the lines of Foulley (1992) would be highly desirable.
- (iv) The implications of more realistic genetic models, *ie* the influence of different distributions of gene effects and frequencies in a finite loci model.

ACKNOWLEDGMENTS

We thank LLG Janss for kindly providing his program, and G Bolet and R Ponzoni for useful comments. The senior author gratefully acknowledges a grant from INRA.

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APPENDIX

Genetic evaluation for 1 continuous and 1 binary trait when there are several observations of the binary variable per record of the continuous trait

Suppose that the number of ova shed is $n_1 + n_0$, with n_1 embryos that survive (litter size = n_1) and n_0 embryos that do not. Ovulation rate is considered as a continuous trait and prenatal survival as a dichotomous trait. There are $n_1 + n_0$ observations of the binary trait for each ovulation record. Breeding values for ovulation rate and embryo survival can be estimated by solving until convergence a system of equations identical to equation [18] in Janss and Foulley (1993) where the weighting vector \mathbf{W} is replaced by

$$\mathbf{W}_A = n_1(v_1^2 + v_1 \mu/\sigma) + n_0(v_0^2 + v_0 \mu/\sigma)$$

if both ovulation rate and litter size are observed or

$$\mathbf{W}_C = n_1(v_1^2 + v_1 \mu/\sigma)$$

if only litter size is recorded. Above

$$v_1 = (1/\sigma)\phi(\mu/\sigma)/\Phi(\mu/\sigma)$$

and

$$v_0 = -(1/\sigma)\phi(\mu/\sigma)/[1 - \Phi(\mu/\sigma)]$$

where σ^2 is the conditional residual variance of embryo survival (Janss and Foulley, 1993, p 185) and μ is the conditional expectation of embryo survival given the location parameters (Janss and Foulley, 1993, equations [8] and [13]).