Original article

Selection for litter size components: a critical review

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Summary – The measurement of component variables such as the number of ova shed (OR) and its inclusion in a linear index with litter size (LS) or prenatal survival has been suggested in order to accelerate genetic progress for LS. Despite optimistic theoretical predictions, however, in no selection experiment has the advantage of including OR in an index as compared to direct selection for LS been convincingly demonstrated. A literature survey shows no clear evidence of changes in genetic parameters with selection. By contrast, genetic drift may suffice to explain the less than expected usefulness of measuring OR, although it is not necessarily the sole cause. It is shown that an approximate figure of how much can be gained by measuring OR relative to direct selection for LS is given by $(1 + \sigma^2_{y_{LS}}/\sigma^2_{y_{OR}})^{1/2}$ with mass selection, where σ^2_y is the phenotypic variance. Nonetheless, the size of the experiment needed to test this prediction is likely to be very large.

litter size / mice / number of ova shed / pig / index selection

Résumé – Sélection des composantes de la taille de portée. Une synthèse critique. *Plusieurs auteurs ont proposé de mesurer le taux d'ovulation (TO) et de l'inclure avec la taille de la portée (TP) dans un indice de sélection (IX) afin d'accroître l'efficacité de la sélection pour TP. Malgré des prédictions théoriques optimistes, aucune expérience de sélection n'a pu démontrer de façon convaincante l'avantage d'une sélection sur l'indice IX par rapport à une sélection directe sur TP. Une revue des expériences de sélection disponibles dans la littérature montre que la réponse plus faible qu'attendue à une sélection sur IX ne peut être expliquée par un changement des paramètres sous l'effet de la sélection, mais pourrait l'être par les effets de la dérive génétique. De façon générale, la formule $(1 + \sigma^2_{y_{LS}}/\sigma^2_{y_{OR}})^{1/2}$, où σ^2_y est la variance phénotypique, donne une estimation réaliste de l'avantage relatif de la sélection sur IX par rapport à la sélection directe sur TP. Malheureusement, des expériences sur un grand nombre d'animaux seraient nécessaires pour vérifier cette prédiction.*

index de sélection / porc / souris / taille de portée / taux d'ovulation

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INTRODUCTION

Reproductive efficiency is one of the most important aspects in a successful animal breeding scheme. Litter size (LS) is the trait responsible for most of the variation in overall reproductive performance in polytocous species and, consequently, LS is given a positive economic weight in all maternal lines of pigs, sheep and rabbits. Its importance has even increased recently in species such as pigs owing to the decreasing economic weight of backfat thickness and, to a lesser extent, of food conversion ratio in the selection goal. Heritability of LS (h^2_{LS}) tends to be low, around 0.10 in pigs (Haley et al, 1988), in rabbits (Blasco et al, 1993a; Rochambeau et al, 1994) and in sheep (Bradford, 1985). Therefore, several authors have sought methods aimed at improving genetic gain in LS using indirect criteria such as hormone levels or number of ova shed (OR) (Johnson et al, 1984; Bodin, 1993). Hormone levels have the advantage that they can be measured in both sexes but their relationship with LS often seems conflicting (Bodin, 1993). In contrast, the number of ova shed always sets an upper limit to LS (provided that identical twins do not exist or are very rare) and is more highly heritable than LS; h^2_{OR} usually ranges from 0.2 to 0.4 (Blasco et al, 1993b). Theoretical results concerning the value of measuring OR have been very encouraging (Johnson et al, 1984). Several experiments have nonetheless questioned these expectations and led to apparent contradictions. Selection on an index combining OR and prenatal survival (PS) has not been shown to be significantly better than direct selection on LS (Kirby and Nielsen, 1993). Direct selection for OR resulted in little or no increase in LS, whereas most of the increase in prolificacy can be explained by an OR augmentation when direct selection for LS has been practised.

The objective of this paper is to review the main selection experiments on litter size components in an attempt to explain the apparent contradictions between theoretical expectations and selection results. Discussion of experimental results will be within the theoretical framework to be presented. Finally, the possible benefits from measuring OR are briefly discussed.

MATERIAL AND METHODS

Theory

Prenatal survival is by definition the proportion of ova shed giving birth to young, ie, PS = LS/OR. Alternatively, LS = OR · PS. Thus genetic parameters for OR and PS determine those of LS. The additive variance in LS $\sigma^2_{g_{LS}}$, genetic covariance between OR and LS ($\sigma_{g_{OR,LS}}$) and PS and LS ($\sigma_{g_{PS,LS}}$) are given, approximately, by

$$\sigma^2_{g_{LS}} \approx \mu^2_{PS} \, \sigma^2_{g_{OR}} + \mu^2_{OR} \, \sigma^2_{g_{PS}} + 2 \, \mu_{PS} \, \mu_{OR} \, \sigma_{g_{OR,PS}} \tag{1}$$

$$\sigma_{g_{OR,LS}} \approx \mu_{PS} \, \sigma^2_{g_{OR}} + \mu_{OR} \, \sigma_{g_{OR,PS}} \tag{2}$$

$$\sigma_{g_{PS,LS}} \approx \mu_{OR} \, \sigma^2_{g_{PS}} + \mu_{PS} \, \sigma_{g_{OR,PS}} \tag{3}$$

(Pérez-Enciso et al, 1994), where μ_i is the phenotypic mean of trait i and g refers to genetic values on the observed scale.

Equations [1] to [3] provide a means of estimating realized genetic parameters from selection experiments. For mass selection on LS, the linear regression coefficient of LS and its components on cumulated selection differentials ($b_{i,\mathrm{CSD_{LS}}}$) can be expressed as

$$
\begin{pmatrix} b_{\mathrm{LS,CSD_{LS}}} \\ b_{\mathrm{OR,CSD_{LS}}} \\ b_{\mathrm{PS,CSD_{LS}}} \end{pmatrix} = \begin{pmatrix} \mu_{\mathrm{PS}}^2 & \mu_{\mathrm{OR}}^2 & 2\,\mu_{\mathrm{OR}}\,\mu_{\mathrm{PS}} \\ \mu_{\mathrm{PS}} & 0 & \mu_{\mathrm{OR}} \\ 0 & \mu_{\mathrm{OR}} & \mu_{\mathrm{PS}} \end{pmatrix} \begin{pmatrix} \sigma_{g_{\mathrm{OR}}}^2 \\ \sigma_{g_{\mathrm{PS}}}^2 \\ \sigma_{g_{\mathrm{OR,PS}}} \end{pmatrix} \Big/ \sigma_{y_{\mathrm{LS}}}^2 = \begin{pmatrix} \Delta g_{\mathrm{LS}} \\ \Delta g_{\mathrm{OR}} \\ \Delta g_{\mathrm{PS}} \end{pmatrix} \quad [4]
$$

where $\sigma_{y_{\mathrm{LS}}}^2$ is the phenotypic variance of litter size, and Δg_i is the genetic change in trait i. When selection is on an index of the type $b_1\,y_{\mathrm{OR}} + b_2\,y_{\mathrm{PS}}$:

$$
\begin{pmatrix} b_{\mathrm{LS,CSD_{IX}}} \\ b_{\mathrm{OR,CSD_{IX}}} \\ b_{\mathrm{PS,CSD_{IX}}} \end{pmatrix} = \begin{pmatrix} b_1\,\mu_{\mathrm{PS}} & b_2\,\mu_{\mathrm{OR}} & b_1\,\mu_{\mathrm{OR}} + b_2\,\mu_{\mathrm{PS}} \\ b_1 & 0 & b_2 \\ 0 & b_2 & b_1 \end{pmatrix} \begin{pmatrix} \sigma_{g_{\mathrm{OR}}}^2 \\ \sigma_{g_{\mathrm{PS}}}^2 \\ \sigma_{g_{\mathrm{OR,PS}}} \end{pmatrix} \Big/ \sigma_{y_{\mathrm{IX}}}^2
$$
$$
= \begin{pmatrix} \Delta g_{\mathrm{LS}} \\ \Delta g_{\mathrm{OR}} \\ \Delta g_{\mathrm{PS}} \end{pmatrix} \quad [5]
$$

where $\sigma_{y_{\mathrm{IX}}}^2$ is the variance of the index. Selection for OR is a particular case when $b_2 = 0$. Realized values for $\sigma_{g_{\mathrm{OR}}}^2$, $\sigma_{g_{\mathrm{PS}}}^2$ and $\sigma_{g_{\mathrm{OR,PS}}}$ can be obtained from equations [4] and [5]. When solutions were out of the parameter space, values minimizing the mean squared differences between left-hand sides and right-hand sides in equations [4] and [5] were used. Statistics for means and phenotypic variances were those in the base population.

Equations [1], [2], and [3] can also be used to predict, approximately, selection responses. From standard results for index selection theory (Falconer and Mackay, 1996) the expected response in LS using an index, IX, combining OR and LS relative to direct selection on LS is, approximately,

$$
\frac{R_{\mathrm{IX}}}{R_{\mathrm{LS}}} \approx \left(1 + \rho_{g_{\mathrm{OR,LS}}}^2 \frac{h_{\mathrm{OR}}^2}{h_{\mathrm{LS}}^2} \right)^{1/2} \quad [6]
$$

with mass selection and one record per individual, where ρ_g is the genetic correlation between traits.

Literature reviews

Two literature surveys were carried out. The first one concerned reported estimates of the pertinent genetic parameters in pigs, mice and rabbits, in order to validate predictions from equations [1], [2] and [3]. In the second literature survey, selection experiments for LS and its components were reviewed. From the experiments where selection was for LS, we analysed only those in which OR had been measured at least in some generation. Selection differentials were converted to mass selection differentials averaged over sexes. Whenever the authors did not provide explicit values for selection differentials or phenotypic means these were calculated, if possible, from the figures.

RESULTS

Results from the first literature survey are given in table I, which shows the estimated and predicted figures for h^2_{LS}, $\rho_{g_{\text{OR,LS}}}$ and $\rho_{g_{\text{PS,LS}}}$. Even if equations [1]–[3] are only first order approximations, agreement between reported and predicted genetic parameters was very reasonable in most instances. The only exception was the Neal et al (1989) experiment, which gave a negative estimate of $\rho_{g_{\text{OR,LS}}}$. However, the realized genetic correlation was positive (see below, table III). Interestingly, predictions from equations [1], [2] and [3] were closer for REML estimates than for estimates by other methods. If we consider that REML estimates are more accurate than Anova-type estimates, this suggests in turn that the above equations might be used to test how 'coherent' the estimates of genetic parameters are from a trait that can be expressed as the product or ratio of two other traits.

Concerning the second literature review, a total of 12 relevant experiments for LS or its components were found (table II). Only three experiments compared simultaneously different selection criteria (references 5, 9 and 10 in table II). These experiments provide most of the information regarding the usefulness of alternative selection methods. The experiment by Kirby and Nielsen (1993) is unique in its duration, 21 generations, and in its reliability, as it was repeated three times. Bidanel et al (1995) compared selection on OR at puberty with what they called corrected PS, actually an index selection comprising PS and OR.

Most experiments listed in table II were aimed at increasing reproductive efficiency, and evidence concerning asymmetrical response can be conveyed only from Falconer's experiments in mice (Falconer, 1960; Land and Falconer, 1969) and more recently from experiments in rabbits (Santacreu et al, 1994; Argente et al, 1997). The experiment in rabbits was for LS but after hysterectomy in order to improve the so-called uterine capacity, and thus their results may not be directly comparable with those for natural LS. Mass or within family selection was used except in Argente et al (1997) and in Noguera et al (1994, 1998) where BLUP evaluation was employed. The use of BLUP certainly accelerates genetic progress but makes the analysis of selection applied more complicated.

Realized genetic parameters were calculated using equations [4] and [5] when enough information was provided by the authors. That was the case in four experiments in mice and pigs (table III). Genetic parameters were computed in the first half and in the whole experiment in order to study their stability, except in Casey et al (1994), where the whole experiment could not be analysed together because index weights were changed in generation 6.

DISCUSSION

We will concentrate on the following issues. a) What is the nature of correlated changes in OR when selection has been practiced on LS? b) How stable are genetic parameters with selection? c) What is the influence of genetic drift on experimental results? d) How close is LS to the optimum selection index?

Correlated changes in the number of ova shed

Correlated and direct responses in OR are at first sight surprising. As table II shows, when selection has been carried out for LS, its increase has been due

Table I. Estimated (predicted) heritabilities (h^2) of litter size (LS), and genetic correlations (ρ_g) between number of ova shed (OR) and LS, and between prenatal survival (PS) and LS in different populations; μ is the phenotypic mean, day is the day of gestation in which survival was observed.

Species	Method	μ_{OR}	μ_{PS}	h^2_{OR}	h^2_{PS}	$\rho_{gOR,PS}$	h^2_{LS}	$\rho_{gOR,LS}$	$\rho_{gPS,LS}$	Day	Ref[a]
Pigs	REML	15.0	0.63	0.30	0.00	—	0.09 (0.08)	0.98 (1.00)	– (–)	Birth	1
	REML	14.3	0.68	0.27	0.08	–0.11	0.14 (0.13)	0.73 (0.69)	0.79 (0.64)	30 d	2
	REML	16.0	0.64	0.24	0.09	–0.34	0.13 (0.11)	0.41 (0.55)	0.70 (0.60)	Birth	3
	REML	16.9	0.75	0.51	0.22	0.02	0.39 (0.36)	0.69 (0.75)	0.73 (0.67)	30 d	4
	Reg[b]	15.0	0.75	0.10	0.13	–0.30	0.32 (0.15)	0.21 (0.40)	0.83 (0.75)	50 d	5
	Reg	14.6	0.75	0.17	0.18	–0.56	0.08 (0.12)	–0.52 (0.28)	0.77 (0.64)	50 d	6
Rabbits	REML	15.2	0.68	0.21	0.23	–0.14	0.29 (0.26)	0.36 (0.39)	0.87 (0.86)	Birth	7
Mice	ANOVA	13.2	0.80	0.33	0.15	0.06	0.18 (0.23)	0.81 (0.68)	0.60 (0.76)	17 d	8

[a] References: 1, Haley and Lee (1992); 2, Bidanel et al (1996); 3, Bidanel et al (1995); 4, Bolet, Bidanel, Gruand and Ollivier (unpublished results); 5, Neal and Johnson (1986); 6, Neal et al (1989); 7, Blasco et al (1993b); 8, Clutter et al (1990); [b] regression of offspring on parent.

Table II. Experiments for litter size (LS) and its components, number of ova shed (OR) and prenatal survival (PS). See the key below for the explanation of the symbols.

Criterion	Species	Type of selection	D	NG	i	n SL	n CL	ΔLS/ΔOR	Ref[a]
LS	Pigs	W	+	11	6.3	107	39	1.00	1
		BLUP	+	1	2.1	202	160	0.70	2
	Mice	W	+/−	31	48.6	37	37	0.94	3
		I	+	11	7.4	33	34	0.95	4
		I	+	21	12.1	70–100	70–100	0.88	5
	Rabbits	IHFS	+	13	6.0	131	60	1.00/0.75	6
		BLUP	+/−	4	?	40	–	1.02	7
OR	Pigs	I	+	9	4.5	39	39	0.11	8
		I	+	4	3.5	45	45	0.11	9
	Mice	IHFS	+	11	10.3	113	34	0.15	10
		I,W	+/−	12	13.4	32	16	0.13	11
IX	Pigs	I	+	10	7.5	150	41	0.45	12
		I	+	4	3.7	45	45	0.72	9
	Mice	I	+	21	13.6	70–100	70–100	0.95	5
PS × LS	Mice	IHFS	+	11	10.3	113	34	1.37	10

Criterion: IX, linear index combining OR and PS. Type of selection: I, individual mass selection; W, within family selection; IHFS, index of full and half sibs; BLUP, best linear unbiased prediction. Direction of selection (D): +, upward; +/−, divergent. NG, number of generations of selection; i, approximate total selection intensity; n, average number of records per generation; SL, selected line; CL, control line; ΔLS/ΔOR, phenotypic ratio of increase in LS versus increase in OR. [a] References: 1, Bolet et al (1989); 2, Noguera et al, 1994, 1998; Noguera and Pérez-Enciso (unpublished results); 3, Falconer (1960); 4, Bradford (1968); Bradford et al (1980); 5, Gion et al (1990); Kirby and Nielsen (1993); Clutter et al (1994); 6, Bolet et al 1990, Brun et al (1992), Rochambeau et al (1994); 7, Bolet et al (1994), Santacreu et al (1994), Argente et al (1997); 8, Zimmerman and Cunningham (1975); Cunningham et al (1979); 9, Bidanel et al (1995); 10, Bradford (1969); Bradford et al (1980); 11, Land and Falconer (1969); 12, Neal et al (1989), Casey et al (1994).

primarily to an OR change ($\Delta LS/\Delta OR \approx 1$) in all species reviewed. Quite to the contrary, when selection was on OR, correlated response in LS was close to nil ($\Delta LS/\Delta OR \approx 0.1$). Bradford et al (1980) described these observations as a "striking example of asymmetrical correlated response".

The fact that the ratio $\Delta LS/\Delta OR$ is close to one for direct selection on LS implies $\sigma^2_{g_{LS}} \approx \sigma_{g_{OR,LS}}$. Note that this condition cannot be fulfilled unless there exists genetic variation for PS because otherwise it would imply that $\mu^2_{PS}\sigma^2_{g_{OR}} \approx \mu_{PS}\,\sigma^2_{g_{OR}}$, ie, $\mu_{PS} = 1$, which is never the case. From the condition $\sigma^2_{g_{LS}} \approx \sigma_{g_{OR,LS}}$, it follows that

$$\rho_{g_{OR,PS}} = \frac{\mu^2_{OR}/z - \mu_{PS}(1 - \mu_{PS})\,z}{\mu_{OR}(1 - 2\,\mu_{PS})} \qquad [7]$$

where $z = \sigma_{g_{OR}}/\sigma_{g_{PS}}$. Further, if we denote $\lambda_{OR} = \Delta LS/\Delta OR$ when selection is on OR, then $\lambda_{OR}\sigma^2_{g_{OR}} = \sigma_{g_{OR,LS}}$, and thus

$$\rho_{g_{OR,PS}} = \frac{(\lambda_{OR} - \mu_{PS})z}{\mu_{OR}} \qquad [8]$$

For typical figures, eg, $\mu_{OR} = 15$, $\mu_{PS} = 0.70$–0.75, $z = 15$–25, equations [7] and [9] predict strong and negative genetic correlations between OR and PS, $\rho_{g_{OR,PS}} < -0.7$.

The number of ova shed increased when selection was on 'corrected' PS (PS + 0.018 OR) in the Bidanel et al (1995) experiment. Here, the condition for OR to increase is $\mathrm{Cov}(g_{PS} + b\,g_{OR}, g_{OR}) > 0$, which implies, $b > -\rho_{g_{OR,PS}}/z$. For extreme negative values of, say $\rho_{g_{OR,PS}}$ less than -0.8, b has to be larger than 0.03. Results in Bidanel et al (1995) hence implied that $\rho_{g_{OR,PS}}$ had a moderately negative value in their population.

The largest ratio, $\Delta LS/\Delta OR = 1.37$, was attained when selecting on what Bradford (1969) called 'adjusted PS', actually $PS \cdot LS$. The breeding value for this trait can be approximated by $\mu^2_{PS}\,g_{OR} + 2\,\mu_{OR}\,\mu_{PS}\,g_{PS}$, and the expected ratio $\Delta LS/\Delta OR$ in this case is, approximately

$$\lambda_{PS\cdot LS} \approx \frac{\sigma^2_{g_{LS}} + \mu_{OR}\,\sigma_{g_{PS,LS}}}{\mu_{PS}\,\sigma^2_{g_{OR}} + 2\,\mu_{OR}\,\sigma_{g_{OR,PS}}} \qquad [9]$$

Substituting equations [1] and [3] into [9] and solving for $\rho_{g_{OR,PS}}$, it follows that

$$\rho_{g_{OR,PS}} \approx \frac{2\,\mu^2_{OR}/z - \mu_{PS}(\mu_{PS} - \lambda_{PS\cdot LS})z}{\mu_{OR}(3\,\mu_{PS} - 2\,\lambda_{PS\cdot LS})}$$

By substituting Bradford's means above and for a range of values of z a strong negative correlation is found again, although out of the parameter space, probably because of the successive approximations involved in [9]. Thus, apparent contradicting results in correlated changes between OR and LS implies that there exists a negatively correlated genetic variation for OR and PS.

Stability of genetic parameters

A common explanation for the less than expected response to selection is that genetic parameters have changed during the selection process (eg, Caballero, 1989).

In this respect the experiment by Nielsen and co-workers (Gion et al, 1990; Kirby and Nielsen, 1993; Clutter et al, 1994) deserves special attention as it is the only work, to our knowledge, where direct selection for LS has been compared simultaneously with a linear index based on OR and PS. The expected advantage of the index based on genetic parameters in the base population (Clutter et al, 1990) was $R_{IX}/R_{LS} = 1.25$, which was close to the observed ratio at the 13th generation, $R_{IX}/R_{LS} = 1.33$, but not in the 21st generation $R_{IX}/R_{LS} = 1.00$. The authors argued that lack of advantage of an index over direct selection in the long term was due to not updating index weights. In principle, the need for updating genetic parameters is more important in this case, as a linear index is only an approximation and optimum weights depend not only on variances but also on means (Johnson et al, 1984).

An assessment of the rate of change in genetic parameters can be deduced from realized genetic correlations, which can be obtained via equations [4] and [5] (table III, reference 1). Two aspects are worth noting. First, there is no evidence that genetic parameters changed dramatically in later generations of selection, which makes it unlikely that not updating the index weights had changed the results very much. Pérez-Enciso et al (1994) showed that the optimum index weight for PS increased with selection but indices were rather robust and not significantly better than direct selection on LS. Second, parameters were similar in both lines and to those estimated in the base population (table I), although h_{LS}^2 was clearly overestimated with respect to the realized value.

Results from the divergent selection for OR (Land and Falconer, 1969) are particularly interesting. In analysing the whole experiment, a clear asymmetric response between upward and downward lines was obtained. A correlated response in the expected direction for LS appeared only in the downward line ($\rho_{g_{OR,LS}} > 0.8$), whereas LS even decreased in the upward line. Falconer (1960) observed an increase in OR in two lines selected for high and low LS, which again indicates an asymmetry in the correlations between OR and LS. Unfortunately, OR was monitored in two generations only, so that $\rho_{g_{OR,LS}}$ can not be accurately determined. Results of selection for OR in pigs are very similar to those in mice. Interestingly, simulation results have shown that measuring OR should be more useful to decrease rather than to increase LS (Pérez-Enciso et al, 1996). These results are due to a non-linear relationship between OR and LS.

Table III shows that, in general, heritabilities are more stable than genetic correlations. All in all, it seems that genetic parameters did not change dramatically with selection. Given the small number of experiments and the sampling errors in estimating realized genetic correlations, though, this conclusion should be taken with caution and differential changes according to selection criteria or in divergent lines cannot be ruled out.

Genetic drift

Assuming that the response is linear, the difference between two lines in generation t is $D_t = t(R_{IX} - R_{LS})$, where R is the response per generation with each criterion, an index or direct selection. The minimum number of generations needed to detect

Table III. Realized heritabilities (h^2) of litter size (LS), number of ova shed (OR) and prenatal survival (PS) and their genetic correlations: h^2_{OR}, h^2_{PS} and $\rho_{g_{OR,PS}}$ were calculated from equations [4] and [5] and h^2_{LS}, $\rho_{g_{OR,LS}}$ and $\rho_{g_{PS,LS}}$, from equations [1], [2] and [3].

Ref[a]	Criterion	Species	Gen[b]	h^2_{OR}	h^2_{PS}	$\rho_{g_{OR,PS}}$	h^2_{LS}	$\rho_{g_{OR,LS}}$	$\rho_{g_{PS,LS}}$
1	LS	Mice	1–13	0.26	0.01	−0.07	0.08	0.94	0.26
			1–21	0.26	0.05	−0.08	0.11	0.78	0.56
	IX[c]	Mice	1–13	0.20	0.05	−0.06	0.09	0.74	0.63
			1–21	0.17	0.05	−0.06	0.08	0.71	0.66
2	IX	Pigs	1–5	0.32	0.10	−0.65	0.12	0.73	0.04
			6–10	0.65	0.10	−0.91	0.11	0.90	−0.64
3	OR	Pigs	1–5	0.55	0.17	−0.80	0.23	−0.57	0.95
			1–9	0.38	0.17	−0.87	0.04	0.15	0.36
4	OR(+)	Mice	1–6[d]	−	−	−	−	−	−
			1–12	0.11	0.20	−0.80	0.23	−0.57	0.95
	OR(−)	Mice	1–6	0.11	0.02	−0.99	0.00	0.84	−0.75
			1–12	0.07	0.01	0.68	0.10	0.94	0.89

[a] References: 1, Gion et al (1990), Kirby and Nielsen (1993); 2, Neal et al (1989), Casey et al (1994); 3, Zimmerman and Cunningham (1975), Cunningham et al (1979); 4, Land and Falconer (1969). [b] Generations over which parameters are estimated. [c] Index combining OR and PS records. [d] Not calculated due to a negative realized response.

significant differences between alternative criteria can then be calculated applying Hill's (1980) formula,

$$\text{Var}\,(D_t) = 2\,(t\,h^2_{LS}/N_e + 1/M)\,\sigma^2_{y_{LS}} \qquad [10]$$

where N_e is the effective size, M is the number of measured records per generation and σ^2_y is the phenotypic variance. Again, the experiment by Nielsen and co-workers is particularly illustrative. Assuming estimated genetic parameters in the base population, average realized selection intensity, $N_e = 37$ (calculated from the average increase in inbreeding over the three replicates) and $M = 100$, it is found that a minimum of 24 generations of selection should have been needed in order to detect significant differences ($\alpha = 0.05$). Thus the experiment may not have been powerful enough to detect differences between criteria and genetic drift is a plausible explanation for the results. An illustration of the impact of drift on experimental power is provided by figure 1. This figure shows the minimum number of generations needed to detect differences between index and direct selection for LS under individual mass selection and different selection intensities and population sizes. The population statistics used are given in table IV and are representative of French Large White pig populations (eg, Bidanel et al, 1996; Blasco et al, 1996), but the numbers in figure 1 will be roughly similar in other populations. It is apparent that, from all the reviewed experiments in table II, only Falconer's (1960) results would have been informative for the sake of comparing different criteria.
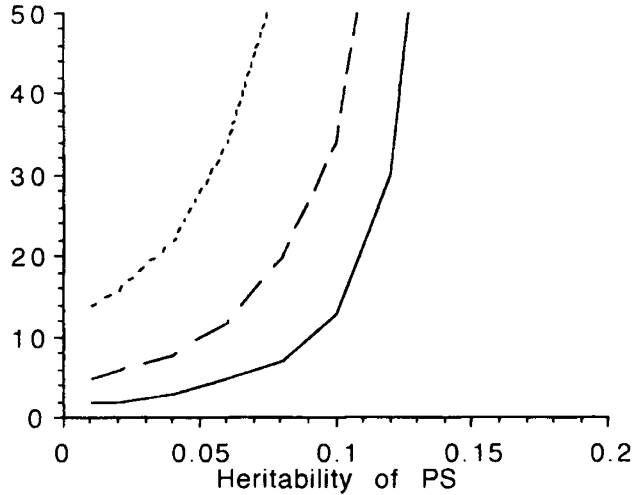
Fig 1. The minimum number, t, of generations of selection needed to detect significant differences between direct selection for litter size and index selection combining litter size and ovulation rate records. Different selection intensities per generation (i), number of records per generation (M), and effective population sizes (N_e) are compared: $i = 1$, $N_e = 20$, $M = 100$ (···); $i = 1.25$, $N_e = 40$, $M = 200$ (– –); $i = 2$, $N_e = 40$, $M = 500$ (—); statistics used are in table IV.

Table IV. Statistics used in figure 1.

Trait	Mean	Variance	h^2
Ovulation rate	15	6	0.30
Prenatal survival	0.7	0.04	Variable
Litter size	10.5	9	0.10

How close is LS to the 'optimum' index?

Litter size can be thought of as a natural index combining OR and PS (Johnson et al, 1984) and it will be the optimum index only if $\rho_{g_{OR,LS}} = 0$, ie, when measuring OR does not convey any information about LS. Otherwise a linear index can be derived such that, in principle, response in LS is larger than with direct selection at least in the first stages of selection. The extent to which LS is close to the 'optimum' index can be assessed by means of retrospective indices. Retrospective weights are defined as $\mathbf{w_R} = \mathbf{G}^{-1}\Delta\mathbf{g}$, where $\mathbf{G}$ is the genetic covariance matrix between OR and PS and $\Delta\mathbf{g}$ is the vector containing changes in these two traits (van Vleck, 1993), ie,

$$\begin{pmatrix} w_{OR} \\ w_{PS} \end{pmatrix} = \begin{pmatrix} \sigma^2_{g_{OR}} & \sigma_{g_{OR,PS}} \\ \sigma_{g_{OR,PS}} & \sigma^2_{g_{PS}} \end{pmatrix}^{-1} \begin{pmatrix} \Delta g_{OR} \\ \Delta g_{PS} \end{pmatrix}$$

Using realized genetic parameters, relative weights $1: w_{PS}/w_{OR}$ were 1:5.3 and 1:10.8 for IX and LS lines in Kirby and Nielsen's (1993) experiment in mice. In pigs, selection on an index (Casey et al, 1994) resulted in a relative weight $w_{PS}/w_{OR} = 8.1$ but had selection been on LS, w_{PS}/w_{OR} would have been 19.5. As expected, optimum index selection is associated with a larger increase in OR than direct selection, but the differences are not dramatic. It is generally accepted that doubling the economic value for one of the traits changes selection efficiency by only a few percent (Weller, 1994).

It can be shown that when selection is on LS,

$$\frac{w_{PS}}{w_{OR}} = \frac{\mu_{OR}}{\mu_{PS}} \qquad [11]$$

(Smith, 1967; Pérez-Enciso et al, 1994), that is, relative changes in its components are independent of genetic parameters. Note that these weights are not constant, as OR and PS means change with selection, and thus LS behaves as a self-adjusted non-linear index. If a linear index combining OR and PS is used, the equivalent expression is:

$$\frac{w_{PS}}{w_{OR}} = \frac{\sigma_{y_{OR,PS}}\,\sigma_{g_{OR,LS}} - \sigma_{y_{OR}}^2\,\sigma_{g_{PS,LS}}}{\sigma_{y_{OR,PS}}\,\sigma_{g_{PS,LS}} - \sigma_{y_{PS}}^2\,\sigma_{g_{OR,LS}}} \qquad [12]$$

Similarity between equations [11] and [12] provides a measurement of how close LS is to an optimum linear index.

GENERAL DISCUSSION AND CONCLUSION

In practice, the animal breeder is mainly interested in how much can be gained by measuring OR. The maximum advantage of including OR occurs when $h_{PS}^2 = 0$, because then OR and LS are repeated measurements of the same trait but at different stages of gestation, ie, $\rho_{g_{OR,LS}} = 1$. In this particular case

$$h_{LS}^2 = h_{OR}^2\,(1+k)^{-1} \qquad [13]$$

(*Appendix*) where $k = \mu_{OR}(1 - \mu_{PS})/\mu_{PS}\,\sigma_{y_{OR}}^2$. Because k is positive, h_{LS}^2 is always smaller than h_{OR}^2 if $h_{PS}^2 = 0$, the smaller μ_{PS} the larger the reduction. The upper limit of the ratio $R_{IX_{MAX}}/R_{LS}$ is $[2 + k]^{1/2}$, which follows from equations [6] and [13]. Similarly, the maximum ratio of indirect response in LS when selecting on OR to direct response, $CR_{OR_{MAX}}/R_{LS}$, is, approximately, $[1 + k]^{1/2}$. For most species and populations, k ranges between 0.6 and 1.5 and thus the theoretical upper limit to relative increase in response with mass selection by measuring OR is about 1.5 and 2 times. In general terms, the larger prenatal mortality and the smaller h_{PS}^2, the larger the value of measuring OR. From the previous analyses, it seems that these optimistic predictions have not been realized owing to a negative genetic correlation between OR and PS, whereas the impact of changes in the genetic parameters is

probably limited. Under the condition $\sigma^2_{g_{LS}} \approx \sigma_{g_{OR,LS}}$, which follows from the fact that $\Delta LS/\Delta OR$ is close to one for direct selection on LS, equation [6] simplifies to

$$\frac{R_{IX}}{R_{LS}} \approx \left(1 + \frac{\sigma^2_{y_{LS}}}{\sigma^2_{y_{OR}}}\right)^{1/2} \approx 1.5$$

for typical figures in polytocous species. Nonetheless, figure 1 suggests that very large experiments are needed in order to test the advantage of index selection over direct selection. Genetic drift may suffice, although it is not necessarily the sole cause, to explain why experiments to validate the theoretical advantage of measuring OR have failed. Note in addition that figure 1 is rather a lower limit for experimental size because a linear response is assumed and that genetic parameters are assumed known without error. Sheridan (1988), observed that realized heritabilities were less than expected in 57% of 198 experiments reviewed and greater than expected in 38% of the cases, which suggests that genetic drift is a common explanation for lack of agreement between theory and experimental results. Bradford remarked in 1980 that 'selection for litter size is remarkably effective, and to date no better selection criterion for improving mean number of young born per litter has been identified'. It seems that this statement has not been convincingly refuted because the size of the experiment needed is likely to be very large.

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APPENDIX: PREDICTION OF GENETIC VARIATION IN LITTER SIZE WHEN HERITABILITY OF PRENATAL SURVIVAL IS NIL

The phenotypic variance of LS in terms of those of OR and PS can be obtained from:

$$\sigma^2_{y_{LS}} = E_x[\text{Var}(\text{LS}|\text{OR} = x)] + \text{Var}_x[E(\text{LS}|\text{OR} = x)]$$

where $\text{Var}(\text{LS}|\text{OR} = x)$ and $E(\text{LS}|\text{OR} = x)$ are the phenotypic variance and mean litter size for $\text{OR} = x$, respectively. In the particular case of no genetic variation in PS, $\text{Var}(\text{LS}|\text{OR} = x) = x\,\mu_{PS}(1 - \mu_{PS})$ and $E(\text{LS}|\text{OR} = x) = x\,\mu_{PS}$, because μ_{PS} is constant for all OR. Thus

$$\sigma^2_{y_{LS}} = \mu_{OR}\,\mu_{PS}(1 - \mu_{PS}) + \sigma^2_{y_{OR}}\,\mu^2_{PS}$$

and

$$h^2_{LS} = \sigma^2_{g_{OR}}\,\mu^2_{PS}/\sigma^2_{y_{LS}} = h^2_{OR}[1 + \mu_{OR}(1 - \mu_{PS})/\mu_{PS}\,\sigma^2_{y_{OR}}]^{-1}$$