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Selection for litter size in pigs. II. Efficiency of closed and open selection lines*

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Abstract – A selection experiment on litter size in the pig was carried on for seventeen generations in an Inra experimental herd. The founder population was made up of 10 males and 120 females from the Large White breed. Selection was first performed for ten generations in a closed line, compared to a control line derived from the same founder population. Selection was carried on within sire family on the total number of piglets born in the first two litters of the dam (TB1 + TB2). After ten generations, the selection criterion became dam TB1 only. The control line was then discontinued and a panel of frozen semen from the 11th generation boars was created for later comparisons. The selected line was opened to gilt daughters of hyperprolific boars and sows, at a rate of 1/8 per generation, and the same selection procedure was applied irrespective of the origin of the gilt. During the whole experiment, the number of ova shed (OS) and the number of live embryos (LE) at 30 days in the 3rd pregnancy were recorded. These two parts of the experiment were analysed using REML estimation of genetic parameters and a BLUP-Animal Model in order to estimate the responses to selection. Significant heritabilities for TB1, TB2, OS and LE were obtained, *i.e.* 0.10, 0.05, 0.43 and 0.19, respectively. Significant common environment variances and covariances were estimated for nearly all traits. Significantly positive BLUP responses per generation were observed from G0 to G17 for TB1 (+0.086), TB2 (+0.078), OS (+0.197) and LE (+0.157). However, the responses were 3- to 4-fold higher in the G12–G17 interval compared to G0–G11, and they were also in fair agreement with previous estimates based on standard least-squares procedures, using the control line and the control frozen semen panel. Since G11, the selection intensity was increased by nearly 80 p. cent compared to the previous generations, and the proportion of hyperprolific ancestry increased up to 65 p. cent in the sows of the last generation. The total genetic gain of

* Second part of Bolet *et al.* [2]

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about 1.4 piglets at birth per litter could be shared between a gain due to immigration, of about 0.8 piglets per litter, and a within-line selection gain of about 0.6 piglets. Thus by combining selection and immigration in the second part of the experiment, advantage could be taken from both the genetic superiority of the immigrants and the higher internal selection intensity made possible by immigration.

pigs / selection / litter size / open line / immigration

1. INTRODUCTION

Several selection experiments for litter size have been conducted in the pig, references of which may be found in Bolet *et al.* [2] and in the review of Rothschild and Bidanel [14]. One of the earliest such experiments was started in 1965 [11] and carried on for seventeen generations in an Inra experimental farm. Selection was first performed in a closed line in comparison with a control line. After ten generations, the selected line was opened to gilts which were daughters of hyperprolific boars and sows. These two parts of the experiment were analysed separately [1,2,13] using standard least-squares methods for evaluating the responses. The objective of this paper is to present a complete analysis of the 17-generation experiment, using Restricted Maximum Likelihood (REML) estimation of genetic parameters, and Best Linear Unbiased Prediction of breeding values under an Animal Model (BLUP-MA). These methods, much more powerful and accurate, allow to combine the information from the two parts of the experiment and to take into account the information on the origin of the hyperprolific animals introduced into the open line. It is then possible to compare the responses to selection in the closed and in the open steps of this experiment.

2. MATERIALS AND METHODS

2.1. Animals

This experiment took place at the Inra experimental farm of Galle, in Avord (Cher) from 1965 to 1987. From a Large White base population of 10 boars and 120 sows (G0), two lines were derived, a selected line (SL) and a control line (CL). The selected line was divided up into 8 families of 1 male (plus one additional male) and 10 females.

From G0 to G11, the two lines were bred simultaneously using natural mating. Oestrus of gilts was detected when they reached 80 kg live weight. Gilts were mated at the first oestrus and, if still not pregnant, at the next oestrus. Group-farrowing over a period of about 3 months was arranged during the whole experiment and replacements were usually selected within first litters, thus allowing a generation interval of about one year. In all generations with the

exception of G14, a random sample of about 30 sows per generation was mated after weaning of the second litter (or the third in G16) and slaughtered 30 days after mating. The number of corpora lutea on the ovaries (which represents the number of ova shed) and the number of live embryos were counted. In the second and subsequent gestations, boars of different breeds were used, mainly Piétrain. The control line (CL), in which a random choice was made within litter for females and within sire for males, was conducted at the same rhythm as SL from G1 to G11. The control line was then discontinued and semen from G11 control males was frozen. After their first two litters, females of the G14 SL were inseminated with 10 of these boars and the daughters from this CLxSL cross were compared to contemporary G16 SL females [2].

2.2. Selection criteria

From G1 to G9, males and females were selected within sire family, on the total number of piglets born in the first two litters of the dam. From G10 onwards, the experimental design was modified to take into account the first results (*i.e.* the low heritability of the criterion of selection and the weak selection intensity [13]) and to possibly apply higher selection intensities. The selection criterion became the size of first litter only. Within-sire selection was maintained for males, but it was changed to across-sire selection for females. The line was opened to gilts which were daughters of hyperprolific sows. These sows were detected in farms through the national recording programme and were also used to constitute a hyperprolific line of boars [9]. The gilts purchased were all inseminated by boars of this hyperprolific line before being introduced into SL, in which they constituted, at each generation, a supplementary sire family. They were subjected to the same selection and mating protocol as the other candidates. This group of immigrant hyperprolific gilts mated to hyperprolific boars was then considered as one of the 8 sire families in each SL generation. Correspondingly, the theoretical immigration rate was about 0.125 (1/8) at each generation.

2.3. Statistical methods

The traits analysed were: total litter size at birth in first (TB1) and second parity (TB2), number of ova shed (OS) and number of live embryos (LE) in third parity. Genetic parameters were estimated using a derivative-free REML procedure applied to a multiple trait individual animal model, with random additive genetic (h^2) and common litter environment (c^2) effects. Generation was fitted as a fixed effect for all traits. Age at mating was fitted as a covariate within parity for litter size. In addition, two groups of ancestors, one non-hyperprolific group and one hyperprolific group, were considered in the model, following the procedure of Westell *et al.* [23]. The analyses were

performed using version 4.2 of the VCE computer package [10]. Standard errors of variance components and genetic parameters were obtained from an approximation of the Hessian matrix when convergence was reached.

Direct and correlated responses to selection were calculated from the estimated breeding values (EBV) of females using a BLUP procedure applied to the same animal model as above. The analyses were performed using the PEST package of Groeneveld *et al.* [4]. The genetic parameters used to estimate the EBVs were those obtained using the REML procedure described above. All these analyses were performed simultaneously on TB1, TB2, OS and LE to estimate the genetic correlations and to take into account the effect of selection on TB1 and TB2 [16]. The average responses to selection were calculated from the regression of individual EBVs of the breeding females on generation number.

The selection differential was calculated as the difference between selected dams and their contemporaries, following the procedure used in a mice selection experiment by Joakimsen and Baker [6]. Dam deviations of generation n were weighted, either by the number of their daughters farrowing in the $n + 1$ generation (dam-daughter path), or by their number of granddaughters (daughters of their sons) farrowing in the $n + 2$ generation (dam-son path).

The inbreeding coefficients and the probability of origin of genes were calculated as described by Vu Tien Khang [20], using the JVT package [21]. The proportion of hyperprolific ancestry was thus obtained, and it provided an estimate of the immigration rate achieved at each generation.

3. RESULTS

3.1. Mean results and genetic parameters

Table I presents the number of breeding animals and parents per generation in the selected line. It also presents, from G10 onwards, the number of hyperprolific (immigrant) females which constituted one of the 8 families. The number of females per generation varied from 50 to 100, around a theoretical number of 80. The immigration rate also varied according to generation, from 0 to 17%, around a theoretical rate of 12.5%. Table II presents the average values, the phenotypic standard deviations and the genetic parameters of the traits analysed. All heritabilities were significantly different from zero, and particularly high values of h^2 were obtained for the physiological components of litter size (OS and LE). Table II also shows significantly positive common litter environment variances (c^2) and correlations for almost all traits.

3.2. Responses to selection

The whole selection experiment (G0–G17) was divided into two periods, namely G0–G11, during which the selected (SL) and the control (CL) lines

Table I. Number of breeding animals, including hyperprolific immigrants, and origins per generation in the selected line.

Generation	Breeding animals			Parents of breeding females	
	Males	Females	Hyperprolific females	Sires	Dams
0	10	82			
1	8	58		10	28
2	8	59		8	28
3	11	57		7	31
4	7	71		11	36
5	8	80		7	27
6	11	60		8	36
7	9	51		7	21
8	10	62		8	25
9	12	65		9	27
10	10	70	8	11	30
11	12	77	3	9	29
12	12	77	5	11	32
13	10	95	9	12	30
14	10	109	0	8	32
15	13	66	11	9	28
16	18	55	2	8	21
17	34	103	0	10	27

were bred simultaneously, and G12–G17, after the discontinuation of CL. It should however be noted that at the end of the first period, namely at G10, immigration had already begun and the selection criterion had been changed to TB1.

Figures 1 to 4 present the trends in breeding values of SL and CL and clearly show an increase in the rates of genetic gain around G10, for the four traits considered. Significantly positive responses per generation were observed for the four traits, and the regressions in SL were 3- to 4-fold higher in G12 to G17 compared to G0 to G11 (Tab. III). In the former period, there was also a significantly positive response in the control line for TB1 and, to a lesser extent, for TB2, whereas no responses were evidenced for the other traits. Fluctuations of environmental effects across generations reaching 4 piglets per litter (not shown in Figs. 1 to 4) could also be evidenced, though no significant trend over generations appeared.

The genetic gains estimated in this paper were compared to those previously published (see Tab. IV), and estimated separately in the two phases of the experiment. Bolet *et al.* [2] used the standard least-squares method to compare

Table II. Number of records, means and standard deviations and genetic parameters.

TB1: 1st litter size

TB2: 2nd litter size

OS: number of ova shed

LE: number of embryos

Columns 4–7: heritabilities and common litter environment effect (\pm standard deviation) on the diagonal, genetic and common litter environment correlations (\pm standard deviation) above the diagonal, residual correlations below the diagonal.

	Number of records	Mean	Phenotypic SD	TB1	TB2	OS	LE
TB1	1 421	9.78	2.97	0.10(\pm 0.03)	0.65(\pm 0.21)	0.63(\pm 0.13)	0.47(\pm 0.21)
TB2	1 285	10.62	3.16	0.06(\pm 0.02)	0.79(\pm 0.28)	0.40(\pm 0.22)	0.38(\pm 0.26)
OS	656	16.82	3.23	0.13	0.05(\pm 0.02)	0.88(\pm 0.15)	0.98(\pm 0.06)
LE	575	12.58	3.81	0.02	0.03(\pm 0.02)	0.77(\pm 0.31)	0.84(\pm 0.26)
				0.08	0.42(\pm 0.07)	0.10(\pm 0.05)	0.63(\pm 0.21)
				0.06	0.13	0.38	0.20(\pm 0.06)
							0.14(\pm 0.06)

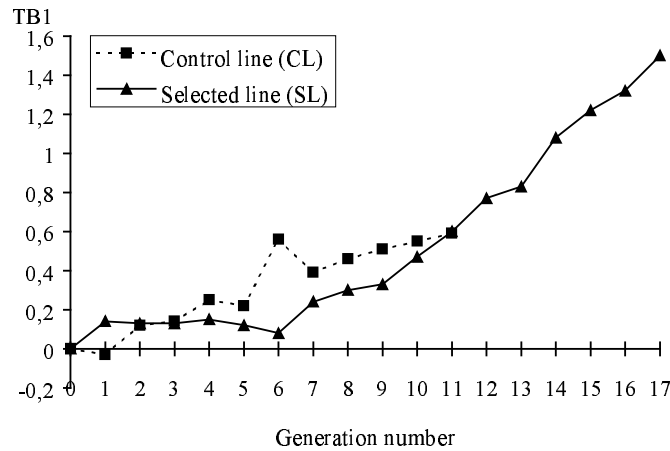


Figure 1. Size of first litter (TB1). Evolution of average generation breeding values, expressed as deviation from G0.

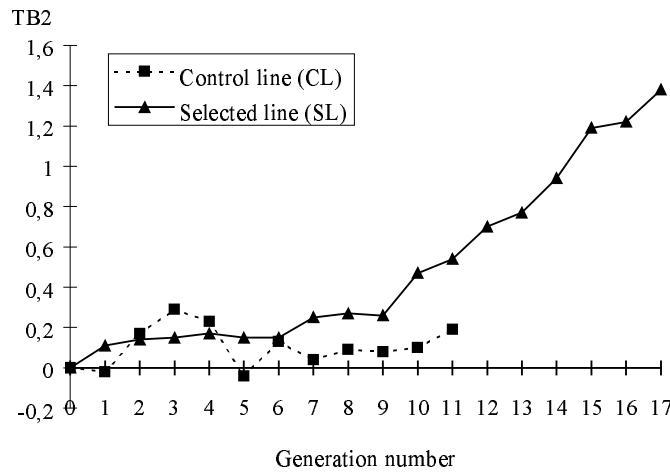


Figure 2. Size of second litter (TB2). Evolution of average generation breeding values, expressed as deviation from G0.

the selected and the control lines during the eleven first generations of selection. In the second phase, Bolet *et al.* [1] estimated the genetic progress in G16 by comparing the selected line to the CLxG14SL cross described in 2.1. and weighting the deviation by 16/9. Assuming a linear evolution of the difference between SL and CL across generations and no heterosis in the cross, the deviation was considered as representing the gain over the remaining nine generations (from G7 to G16), *i.e.* 9/16 of the total gain. The present estimates agree rather closely with the least-squares estimates over the G0–G11 period. Direct responses were weak, though significant indirect responses

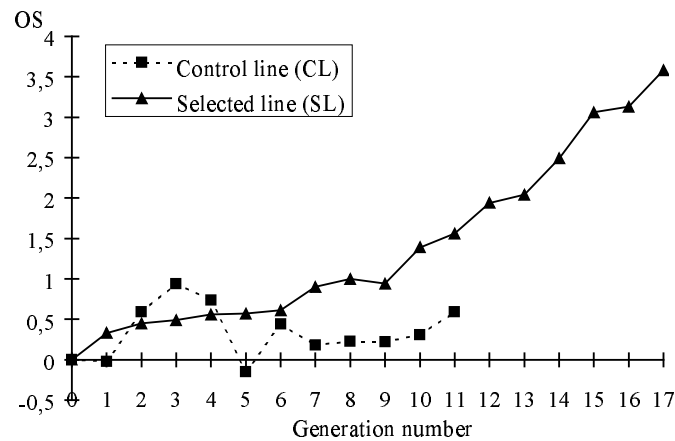


Figure 3. Number of ova shed during third pregnancy (OS). Evolution of average generation breeding values, expressed as deviation from G0.

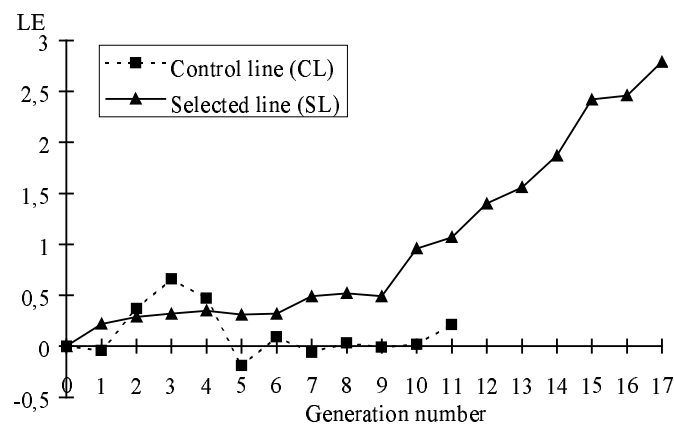


Figure 4. Number of live embryos at 30th day of third pregnancy (LE). Evolution of average generation breeding values, expressed as deviation from G0.

were shown for both OS and LE. Over the whole experiment, the total least-squares responses were considerably higher for TB2 than for TB1, though the BLUP-AM estimates were about equal for the two traits, and similar total responses (TB1 + TB2) were estimated by both methods. Significant responses were also observed for OS and LE with both methods, though the least-squares estimates were considerably lower.

3.3. Selection differentials

Table V compares the selection differentials achieved in both phases of the experiment through the dam-son and dam-daughter pathways. When these

Table III. Response to selection: regression of estimated breeding values (EBVs) on generation number.

	TB1	TB2	OS	LE
SL G0–G17	0.086 (0.002) **	0.078 (0.002) **	0.197 (0.006) **	0.157 (0.005) **
SL G0–G11	0.044 (0.004) **	0.039 (0.004) **	0.121 (0.011) **	0.078 (0.008) **
SL G12–G17	0.151 (0.010) **	0.144 (0.011) **	0.348 (0.031) **	0.293 (0.024) **
CL G0–G11	0.058 (0.006) **	0.010 (0.005) *	0.029 (0.015) ns	0.001 (0.011) ns

ns: not significant. * $P < 0.05$. ** $P < 0.01$.

Table IV. Comparison of estimations of genetic gain in this study and in previous papers using least-squares methods.

	G0–G11 (rate per generation)		Overall gain	
	SL–CL (1)	SL (2)	G0–G16 (3)	G0–G17 (4)
TB1	–0.03 ns	+0.044 **	+0.55 ns	+1.50
TB2	+0.05 ns	+0.039 **	+2.24 †	+1.38
OS	+0.12 *	+0.121 **	+1.95 ns	+3.58
LE	+0.12 **	+0.078 **	+1.95 ns	+2.79

(1) Bolet *et al.* (1989).

(2) EBVs in this study (see Tab. III).

(3) Least-squares estimates of Bolet *et al.* (1987).

(4) EBVs in this study (see Figs. 1–4).

ns: not significant. † $P = 0.10$. * $P < 0.05$. ** $P < 0.01$.

were converted into selection intensities, taking into account the change in the selection criterion in G11, it appeared that selection intensity was more than doubled in the dam-daughter pathway against an increase of 64% in the dam-son pathway.

3.4. Probability of origin of genes and inbreeding

In the line selected since G11, hyperprolific genes entered *via* the regular immigration of hyperprolific gilts and boars. Genes in the females of each generation could then be traced either to a prolific or to a non-prolific origin.

Table V. Average selection differentials and selection intensities per generation.

	Dam-daughter		Dam-son	
	G0–G10 ⁽¹⁾	G11–G16 ⁽²⁾ (SL)	G0–G10 ⁽¹⁾	G11–G16 ⁽²⁾ (SL)
Selection differential				
SL	2.13	2.09	2.89	3.90
CL	0.72	–	0.68	–
SL-CL	1.41	–	3.49	–
Selection intensity (SL-CL)	0.33	0.71	0.81	1.33
Equivalent selection rate (%)	0.81	0.56	0.49	0.23

⁽¹⁾ Selection differentials for TB1 + TB2.

⁽²⁾ Selection differential for TB1.

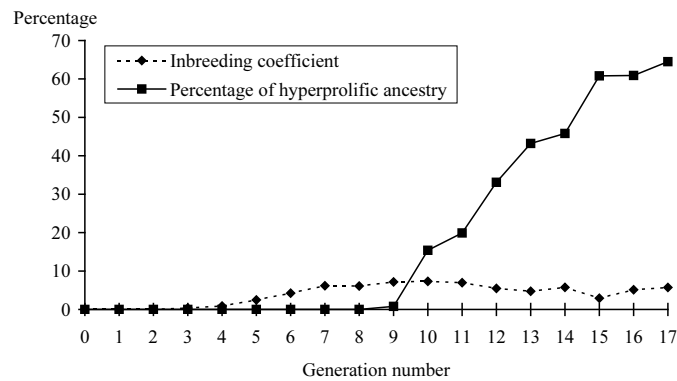


Figure 5. Percentage of hyperprolific ancestry and inbreeding coefficient of the SL females in each generation.

Figure 5 shows that the proportion of hyperprolific ancestry increased up to an average proportion of 65% prolific genes in the sows of the last generation.

In the control line, the inbreeding coefficient of sows increased to about 10 percent in G11, as also shown in Bolet *et al.* [2]. In SL, it reached a maximum value of about 7% in G9–G10 (see also [2]) and decreased slightly thereafter, as a consequence of immigration, as shown in Figure 5.

4. DISCUSSION

4.1. Genetic parameters

The parameters of Table II for litter size are in agreement with the values found in the literature (see the review by [14]). However the h^2 values of OS and

LE were quite above the usual estimates. A significant common litter environment effect (c^2) was found for all traits, except TB2. This is in agreement with several other observations, including those of Strang and Smith [17], of much larger full-sib heritabilities compared to half-sib or daughter-dam estimates, though, in contrast, Haley *et al.* [5] concluded to remarkably similar estimates for all methods. It is known that the variation covered by c^2 in a purely additive genetic model includes various effects such as dominance and maternal genetic effects, in addition to purely environmental effects. The evidence on maternal heritability is controversial, as underlined by Rothschild and Bidanel [14], and this may partly be a consequence of the difficulty in disentangling the effects included in the common litter factor. When these results are compared to those previously published [2], there is no evidence of a reduction of genetic variability during the experiment. However, this is to be expected since the parameters of Table II refer to the base population under the animal model used. However, when G0–G10 and G11–G17 were analysed separately, a decrease in genetic variance was observed, except for TB1. The reduction varied according to the trait considered, much more for OS and LE than for TB2. No definite conclusion can be reached because of the limited size and duration of the experiment.

4.2. Selection responses

Significant responses were observed for all traits in the selected line. From G0 to G11, the regression of estimated breeding values on generation number were low, but significantly positive. Genetic progress from G12 to G17 was much higher. There was a fair agreement between the response patterns based on EBVs and those obtained by comparison with the control line cross CLxSL, though some differences can be noted between the actual estimates in Table IV. It can also be noted that the average accuracy of female EBVs for TB1 was 0.45, which is about 42% above the accuracy of TB1 itself, the actual selection criterion used in the experiment. This leads us to suspect that a much higher selection response would have been obtained using BLUP, though the *a posteriori* EBV includes information on TB1 and TB2 and is not quite compatible with the selection procedure applied.

The use of EBVs and their prediction errors to derive estimates of selection responses has been a matter of debate for many years. Thompson [18] pointed out that the responses derived from mixed models include information components based on the selection pressure applied. As a consequence, such responses are highly dependent on the genetic parameters assumed in the model, as shown for some simple experimental designs by Thompson [19], Sorensen and Johansson [16] and Ollivier [12]. The Bayesian approach advocated by Sorensen *et al.* [15] obviates this difficulty, though it leaves open the question of choosing appropriate priors and the incidence of this choice on the variance

of the estimates. The procedure applied in the present paper followed the classical approach of Gianola *et al.* [3], which offers a good approximation to the full Bayesian approach when the information on heritability provided by the data is sufficient. This can be assumed to be the case here, though the data on OS and LE are somewhat limited (Tab. II). A likely explanation for the higher responses from EBVs of these two traits may therefore simply be the result of the high values of h^2 assumed for them, as reported in 4.1.

Another issue is the genetic model assumed. It is well known that ignoring dominance for traits known to exhibit such effects, like litter size in pigs, leads to an overestimation of the responses, as shown for instance very clearly by the simulations of Johansson *et al.* [7]. However, as these authors show, the bias is reduced when the animal model includes a litter effect, both for estimating heritability and EBVs, as was done here.

4.3. Role of immigration in the responses observed

An important point to be discussed is the origin of the genetic progress observed in the second phase of the experiment and the respective roles of selection and immigration in the improved efficiency of the experiment.

First, quite independently from the immigration protocol, the change of selection criterion, from TB1 + TB2 to TB1, allowed a more intense selection because there were more sows with only one litter than with two successive litters. Second, the selection intensity was increased by changing the selection method for females, from within-family selection to purely mass selection. These two sources of increase are reflected in the comparisons of Table V. The increase of 79 per cent in the overall selection intensity was made possible at no extra inbreeding cost, as shown in Figure 5.

Selection with immigration has been shown by Webb [22] to be biased as a result of (i) possible heterosis in the cross between immigrants and natives, and (ii) treating natives and immigrants as if they were members of the same population, which tends to underrate superior immigrants. Source (i) is unlikely in our experiment, since there is no cross initially and also since both populations are Large White. Source (ii) deserves more attention since it may affect dam selection in our experiment and would thus tend to underrate the hyperprolific dams. However, hyperprolific gilts tend to express little of their genetic superiority in their first litters [8], and we can consider that immigration had little influence on the selection of females. This is also confirmed by the actual proportion of hyperprolific ancestry in G17, which is quite close to its expectation ($1-0.875^7$) under a pure immigration scheme at a rate of 0.125 for seven generations. However, considering that the actual immigration rate was lower than intended in the experimental design (Tab. I), this assumption has to be qualified.

The following tentative interpretation of our results can then be presented, if we assume no interaction between selection and immigration. The total genetic gain of about 1.4 piglet at birth per litter (average of TB1 + TB2) can be partly attributed to immigration and the remainder to selection. Assuming a genetic superiority of 1.6 piglets in hyperprolific females [8], taking the 0.65 proportion of hyperprolific origin reached in G17 (see Fig. 5), and given that the immigrant piglets are 75% hyperprolific, the gain due to immigration may be estimated to be about 0.8 piglets, slightly above half of the total gain. Though the remaining selection gain of about 0.6 piglets is somewhat below the gain which could be expected for TB1 from the selection intensities applied over G11–G16, it can be concluded that, by combining selection with immigration in the second part of this experiment, it has been possible to benefit both from the immigrants superiority and from a more efficient within-line selection than in the closed line of limited size used in the first part of the experiment.

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