

RESULTS OF A LONG-TERM SELECTION EXPERIMENT FOR LEAN TISSUE GROWTH IN THE PIG.

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SUMMARY

An account is given of a pig selection experiment begun in 1965 at the INRA artificial insemination center of Rouillé (Vienne) France. Altogether 20 successive Large White boar generations (1965-1984) have been compared, namely 179 boars tested on 5985 progeny from 1966 to 1985. The boars were selected on a performance-test index including growth rate and backfat thickness. Selection responses were measured for growth, feed efficiency, carcass traits and meat quality, by using a "repeat-sire" design and applying mixed model methodology (except for feed efficiency measured on a pen basis). Estimated annual genetic trends over boar generations are 6.4g lean/day ($P < .001$) and $-.30$ kg feed/kg lean ($P < .01$). Daily feed intake has been slightly increased ($P < .1$) and an unfavourable indirect response in meat colour ($P < .001$) is to be noted. Higher responses were generally observed over the second half of the experiment, as expected from the increase in boar selection intensity. Also, generally lower responses were obtained over dams, compared to sires of the same year, though the lag between them tended to become smaller in the more recent years. Those results are discussed in relation to the testing and selection system applied in the experiment.

INTRODUCTION

The efficiency of performance-test indices in the genetic improvement of pig production traits is nowadays widely recognised, and the application of such indices has substantially contributed to increase the efficiency of pig meat production. This has been demonstrated by a few selection experiments, the first and the longest one being the Belstville experiment on high and low backfat thickness (Bereskin et al., 1975). On the other hand, the index approach has been questioned and the choice of a proper testing environment has been much emphasised over the last decade (see Webb and Curran, 1986). I shall here present the results of a pig selection experiment initiated in France in 1965 and still presently continued. The last results obtained in 1985 allow a comparison of 20 generations of boars selected on a growth-backfat index, under a rather constant testing and selection system.

MATERIAL AND METHODS

Experimental design.

The experiment began in November 1965, with the initial inseminations of 10 Large White boars, considered as the founding generation. Young males born from these boars in March 1966 were grouped in the experimental farm of Rouillé (Vienne, France) and selected on their performance-test results

as described below, in order to start inseminations with a new boar generation in November 1966. From then on, a similar operation was renewed each year, i.e. initial inseminations in November with a new generation of selected boars born in March of the same year. So these were sons of the boars selected the previous year (and also partly, since 1977, of boars selected 2 years before) and of sows randomly chosen in the insemination zone. However, in 1983 and 1984, the line was opened to outside contemporary boars. These originated from the French Large White herdbook and were selected among top ranking boars in the national performance-test stations, about 2 standard-deviations above contemporaries.

Responses to selection were continuously monitored through a so-called "repeat-sire" system. Such a design was initially proposed by Dickerson (1960) as a simplification of the "repeat-mating" design of Goodwin et al. (1955). Each year, in parallel to the performance-testing of young males, progeny from 2 successive generations of boars (those selected the year before and those selected 2 years before) were simultaneously tested. The details of the experimental design are given elsewhere (Ollivier 1977 and 1980) for the period 1966-1976, during which genetic responses were measured on females and castrated males. In 1977, testing of castrates was discontinued and the boar candidates were included in the design in order to measure responses also for the selection criteria in addition to the previously considered traits which were then only measured on females (see below).

During the period considered, 175 boars from within the line have been progeny-tested, out of which 129 have been repeated the following year and 6 after a delay of 5 years by use of frozen semen, and in addition 4 "outside boars" have been compared to the selected line (table 1). Selection responses have been measured on 2976 females, 1301 castrates and 1708 boars.

Management and data collection.

Each year in May, pigs are bought, at about 20 to 25 kg liveweight, from 50 to 70 different farms serviced by the experimental A.I. center of Rouillé (Vienne, France). They are then penned in groups of about 10 pigs/pen by generation, with free access to a pelleted diet in self feeders and to water. Consequently, feed intake is recorded per pen, allowing measure of daily feed intake, daily gain and feed efficiency on a pen basis. Feed composition has remained relatively uniform over the whole experiment, i.e. 15 to 17% crude protein and 3.0 to 3.2 Mcal DE/kg, and the same diet has been given to boars, castrates and females.

Boar candidates have been selected on the following 2 performance-test indices :

$$I_1 = 10 \text{ ADG} - 6 \text{ FCR} - .8 \text{ BF from 1966 to 1968} \quad (1a)$$

$$I_2 = 10 \text{ ADG} - .5 \text{ BF from 1969 to 1984} \quad (1b)$$

where ADG is average daily gain (kg), FCR feed conversion ratio (kg feed/kg gain) and BF average of six backfat measurements (mm), the test period being 30-80 kg, extended to 85 kg in 1977.

Selection responses have been measured for : (1) individual growth, carcass and meat quality traits on females (from 1966(*) to 1985) and castrates (to 1976), over a 30-100 kg test period, (2) individual selection criteria of the boars (ADG and BF) since 1977, (3) pen averages for daily gain per pig

(*) meat quality only measured from 1969 on

(ADG), feed conversion ratio (FCR) and daily feed intake per pig (DFI), over a 30-80 kg test period, extended to 85 and 100 kg in 1977.

In addition, 3 synthetic variables, combining the above ones, have been considered. Lean content (LEAN) is estimated as a linear combination of carcass weight (CAR) at 100 kg liveweight, 2 lean cuts (HAM and LOIN) and the backfat cut (BFC) in a half-carcass (see Ollivier, 1980), such as :

$$\text{LEAN (percent of liveweight)} = .1882 \text{ CAR} + 1.43 \text{ HAM} + 1.66 \text{ LOIN} - 1.53 \text{ BFC} \quad (2a)$$

From this estimation, lean tissue growth rate (LTGR) and lean tissue feed conversion (LTFC) are derived according to Fowler et al. (1976):

$$\text{LTGR (kg/day)} = (\text{ADG} \times \text{LEAN}) 10^{-2} \quad (2b)$$

$$\text{LTFC (kg feed/kg lean)} = (\text{FCR} / \text{LEAN}) 10^2 \quad (2c)$$

More details on the various traits measured are given by Ollivier (1977).

Statistical analyses.

Boar selection is evaluated each year on the basis of the observed within year-building selection differentials for ADG and BF. These are transformed into coefficients of index in retrospect, following the technique originally proposed by Dickerson et al. (1954), and previously applied in the first part of this experiment (see Ollivier, 1985, p.485). For the second period, the within year-building phenotypic variance-covariance matrix used is estimated on the 1708 boars tested from 1977 to 1985.

Selection responses are estimated separately for each of the 3 previously described sets of variables. The following mixed linear model is assumed in analysing the 1st set :

$$y_{ijklmn} = \mu + s_i + b_j + g_k + V_{k1} + m_m + E_{ijklmn} \quad (3a)$$

where μ is the mean, s_i a sex effect (female or castrate), b_j a year-building effect ($j=1\dots,66$) for growth and carcass traits and date of slaughter effect ($j=1\dots, 183$ (155 for one trait)) for meat quality traits, g_k a boar generation (origin) number ($k=1\dots,20$ for the within-line boars and $k=21$ for the Large White herdbook boars), V_{k1} a within generation sire effect, with variance σ^2_V , m_m a dam year of birth effect ($m=1960\dots, 1983$), E_{ijklmn} the residual error, with variance σ^2_E , with V and E considered as random effects, the others fixed.

The same model without the s effect is assumed for the 2d set of variables, i.e. boar ADG and BF. The variances σ^2_V and σ^2_E used in model (3a) are the sire and within-sire components of variance estimated on the data from 1965 to 1975 (Ollivier, 1983 p.101). For LEAN and LTGR heritabilities of .5 and .3 respectively are assumed. The mixed model procedure of Lundehein and Eriksson (1984), adapted by D. Boichard (personal communication) has been used.

The 3rd set of variables (pen ADG, FCR and DFI) is analysed under the following fixed model :

$$z_{ijk1} = \mu + r_i + b_j + g_k + b_1 w_{ijk1} + b_2 w'_{ijk1} + b_3 d_{ijk1} + E_{ijk1} \quad (3b)$$

where r_i is the pen sex-ratio ($i=1$ for 0 to 9 percent castrates, 2 for 10 to 19, etc..., 10 for 90 to 100 percent and $i = 11$ for boar pens), b_1 a linear regression on average pen initial weight w_{ijk1} , b_2 a linear regression on average pen final weight w'_{ijk1} , b_3 a linear regression on the number d_{ijk1} of pigs discarded, and μ, b, g, E defined as in (3a).

Linear trends are derived from the above analyses by regressing the g and m estimates on the appropriate generation or year number, and taking into account the variances and covariances of the estimates considered. Sire and dam annual genetic trends are obtained by doubling the respective regression coefficients for set 1 and set 2. Only sire trends can be estimated for set 3. The group of herd book boars is excluded from all estimations of genetic trends.

RESULTS

Boar selection.

Tables 1 and 2 summarise the selection history of the line. They show an important increase in selection intensity, in the 2d period 1975-1984 compared to the first period 1966-1974, which is due to a larger number of boar candidates tested each year. The ratio of achieved to potential selection intensity has also been improved, as a consequence of a change from a within-sire family selection applied initially to purely mass selection in 1972. The indices in retrospect indicate a tendency to apply a higher weight than intended to ADG in choosing the boars.

Selection responses.

1) Growth and carcass

The estimates obtained for growth and carcass traits, using model (3a), indicate very highly significant linear genetic trends over sire generations for all traits except carcass weight (table 3). Lower and less significant trends are obtained over dam cohorts, especially for carcass traits. In fact, the dam trend in lean tissue growth rate is about 2/3 of the sire trend, whereas in percentage lean the dam trend is below 1/5 of the sire trend and does not reach significance. Responses per sire generation are given in fig.1 for body composition and in fig.2 for liveweight and lean tissue daily gains.

Sire and dam genetic trends for boar traits, estimated over the 2d part of the experiment, confirm the preceding comparisons for fatness, i.e. a markedly higher sire trend in BF, but not for daily gain, for which the sire trend is slightly negative (table 4).

2) Feed efficiency

The estimates derived from model (3b) indicate highly significant sire genetic trends for liveweight and lean tissue feed conversion over the whole experiment. These trends are confirmed in the 2d part of the experiment over a test period extended to 100 kg (table 5). A positive trend in daily feed intake per pig is also worth mentioning, though not significant. Linear trends for pen daily gain tend to indicate a lower response in the 2d part of the experiment. Responses per generation for the 2 feed efficiency traits are illustrated in fig.2.

3) Meat quality traits.

The estimates of sire genetic trends are very highly significant for reflectance, indicating that meat tends to become paler over generations, and for water holding capacity, which is improved, whereas pH24 remains unchanged (table 6). However, dam trends confirm the above tendencies only for meat colour, as a significantly negative trend is obtained for pH and a slightly negative trend for water holding capacity.

4) Comparisons to herdbook boars.

The genetic levels of the herdbook boars are given in fig. 1 and 2, comparatively to the last 2 generations of selected boars. These appear to be superior in lean tissue growth and about equal in lean tissue feed conversion. Consequently, a higher daily feed intake (about .2 kg) is observed in the selection line. Differences in meat quality traits, not reported here, are negligible.

GENERAL DISCUSSION AND CONCLUSIONS

The results of the first part of the experiment reported here have been discussed previously (Ollivier, 1980) and the following discussion will therefore emphasize differences and complements to the first analysis. The model (3a) used here differs from the one applied to analyse the first decade (Ollivier, 1977) in that the simple least-squares methodology with fixed generation effects has been replaced by a mixed model methodology with random sire effects. The latter has well-known advantages, the main ones being (1) to minimise the risk of biases in trends which may result from sequential selection and (2) to reduce the downwards bias in sampling variance inherent to the least-squares approach (see Sorensen and Kennedy, 1984). The first advantage is particularly valuable when evaluating responses in national herds, and consequently mixed model methodology is now currently used in such cases : see Tixier and Sellier (1986) for an application to French breeding herds and for references to similar studies in other countries. The design used in this experiment in principle eliminates any selection bias in estimating sire genetic trends and this appears to be verified by the reasonably good agreement obtained between the estimates derived from the 2 models applied to the same data. However, as the model does not take into account the relationships between sires, sampling variances are still underestimated. Constant between-sire variances have also been assumed in the model, in spite of the reduction entailed by the increase in selection intensity (see table 2), at least for the variables most closely correlated with the selection index. As to dam trends, estimation biases are not to be excluded, as individual dam effects are not considered in the model. Therefore the dam trends are estimated under the assumption of no selection of sows kept to older age. Another potential source of bias could be age of dam effects.

Fig. 1 and 2 show that the estimated linear trends do not always adequately reflect the actual selection responses. For several variables an increase in slope during the experiment is quite evident, particularly for the dam responses in lean content (graph not given here). Such an increase is indeed to be expected, as a consequence of the increase in selection intensity during the experiment and also of a slight reduction in generation interval due to a decrease in age of sows in the population. The estimated "selection effort" (boar selection intensity/generation interval) has indeed increased from .3 for the first 3 years of the experiment to 1.1 in the last 3 ones.

In spite of the above restrictions, which have to be borne in mind when one compares sire and dam trends, a broad agreement in the directions of responses appears for most variables, and also generally larger responses over sire generations as compared to dam cohorts. In 2 cases only (boar daily gain and pH 24) are significant dam trends obtained with opposite, however low and not significant, sire trends. It also appears that the differences observed between sire and dam trends in the first part of the experiment have been noticeably narrowed since, especially for liveweight and lean tissue growth. As pointed out previously (Ollivier, 1980), those differences are partly due to the longer time interval considered for dams, which includes 6 years prior to the first boar selection, and partly to the selection scheme which induces a genetic lag between sires and dams born in the same year. The latter point has been recently discussed in detail (Ollivier, 1985), especially in view of the lack of accurate information on the amount of immigration into the sow population under insemination and on the selection actually applied in sow replacement. For those reasons, reliable estimates of realised heritabilities may be difficult to obtain with the design used here.

The results presented, which cover a period of 2 decades of selection, confirm the general conclusions of the first decade (as summarised by Ollivier, 1985) on the efficiency of the simple growth-backfat index selection in improving simultaneously lean growth and efficiency. Those conclusions also generally agree with the responses obtained in a few similar, though shorter-term, selection experiments, such as those of Webb and King (1976), Sather and Fredeen (1978), Vangen (1979) and Vögeli et al. (1983).

On the other hand, well established genetic parameters in various pig populations over the world confirm the above conclusions, but they also indicate that a substantial gain in selection efficiency can be obtained by including feed conversion ratio as an additional selection criterion. Nevertheless, the simpler growth-backfat index is often recommended in practice. Moreover it has been suggested that undue emphasis on feed efficiency might have detrimental side-effects, such as a reduction of appetite. This also raises the question of the choice of an optimal test environment, as frequently discussed in the last 10 years : see, for instance, Fowler et al. (1976), Smith and Fowler (1978), Fredeen (1980), and Webb and Curran (1986). In that context, the comparison to the 4 herdbook boars realised here (see fig. 1 and 2), though limited in scope, is of some interest, as these boars have been selected in the French central test stations, on an index giving a high weight to feed efficiency. Their lower daily feed intake, as well as the slight tendency to an increase in the selected line, would indicate a difference in response according to the test environment and selection criterion applied.

The unfavourable correlated response in meat colour confirms the tendency observed over the first 10 generations. In contrast, the other 2 meat traits pH and water-holding capacity, do not appear to have been adversely affected. Though halothane testing was not performed in this experiment, there is no indication of the presence of or of an increase in the halothane gene frequency, in contrast to the results of Vögeli et al. (1983). This probably reflects differences in the base populations of the 2 experiments (Landrace in the latter experiment) and also indicates that different genetic mechanisms may account for variation in meat quality, and particularly colour.

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Table 1
Number of boars used in the experiment.

Boars (*)					
Year of birth	T	S	R1	R5	HB
1965	-	10	6		
1966	52	10	9		
1967	50	10	8		
1968	51	10	7		
1969	73	10	10		
1970	78	10	8		
1971	97	8	8		
1972	115	8	7		
1973	99	8	8		
1974	116	10	4		
1975	119	7	5		
1976	104	10	7		

1977	219	11	7	6	
1978	234	8	9		
1979	148	10	9		
1980	195	7	7		
1981	180	8	3		
1982	192	8	4		
1983	218	6	3		2
1984	143	6	-		2

TOTAL	2473	175	129	6	4

(*) T : tested S : selected R1 : repeated in year n+1
 R5 : repeated in year n+5 HB : boars from the French Large White herdbook.

Table 2 : Selection indices and intensities applied in boar selection.

Years of selection	1966-1974		1975-1984	
Boars selected/Boars tested	84/731		81/1715(*)	
Selection intensity				
potential (1)	1.69 (100)		2.09 (100)	
achieved (2)	1.10 (65)		1.79 (86)	
Index coefficients	ADG	BF	ADG	BF
intended (3)	10	-.5	10	-.5
in retrospect	9.6	-.34	15.4	-.65
Relative weight of BF in index (4)				
intended	1.4		.8	
in retrospect	1.0		.7	

- (1) assuming a normal distribution of the selection criterion and mass selection
(2) on index in retrospect (see text)
(3) as given in (1b). ADG : average daily gain - BF : backfat thickness
(4) absolute value of BF coefficient/ADG coefficient, with BF and ADG expressed in standard-deviation unit of the corresponding period.
(*) progeny of R5 boars excluded.

Table 3 : Annual genetic trends (\pm s.e.) for growth and carcass traits.
(test period 30-100 kg).

Trait (*)		Sire annual genetic trend (1965-1984)	Dam annual genetic trend (1960-1983)
ADG	kg	.011 \pm .002 ***	.009 \pm .003 **
CAR	"	-.033 \pm .042 ns	.049 \pm .044 ns
HAM	"	.040 \pm .011 ***	-.003 \pm .011 ns
LOIN	"	.117 \pm .017 ***	.043 \pm .016 **
BFC	"	-.180 \pm .026 ***	-.028 \pm .021 ns
LEAN/CAR	%	.71 \pm .08 ***	.13 \pm .08 +
LTGR	kg/day	.0064 \pm .009 ***	.0042 \pm .0008 ***

- (*) ADG : average daily gain - CAR : carcass weight - HAM : weight of ham - LOIN : weight of loin - BFC : weight of backfat cut - LEAN/CAR : percentage lean in carcass - LTGR : lean tissue growth rate. + $P < 0.10$, ** $P < .01$, *** $P < .001$, ns $P > .10$.

Table 4 : Annual genetic trends for boar selection criteria
(test period 30-85 kg)

Trait (*)		Sire annual genetic trend from 1975 to 1984	Dam annual genetic trend from 1970 to 1983
ADG	kg	-.002+0.004 ns	.014+0.006 *
BF	mm	-.38 ±0.08 ***	-.02 ±0.04 ns

(*) ADG : average daily gain - BF : average of 6 ultrasonic backfat measurements.
*P < .05, *** P < .001, ns P > .10

Table 5 : Annual sire genetic trends for feeding traits.

Trait (*) (pen average)	Test period years	30 - 80 (85)kg 1965 - 1984	30 - 100 kg 1975 - 1984
FCR	kg feed/kg gain	-.048 +.018**	-.034+.017*
LTFC	kg feed/kg lean	-.30 ±.10 **	-.25 ±.10 *
DFI	kg/day	.029 ± 0.017+	.008±.018ns
ADG	kg/day	.019 ± 0.007**	.011±.007ns

(*) FCR : feed conversion ratio - LTFC : lean tissue feed conversion - DFI : daily feed intake per pig - ADG : average daily gain per pig.
+ P < .10, * P < .05, ** P < .01, ns P > .10

Table 6 : Indirect responses in meat quality traits

Trait (*)	Sire annual genetic trend from 1967 (1969 for WHC) to 1984	Dam annual genetic trend from 1962 (63 for WHC) to 1983
PH24 pH unit	.000+0.002 ns	-.014+0.007 *
REF reflectance unit	.87 ±.16 ***	.58 ±.21 **
WHC sec	3.4 ±.8 ***	-1.5 ±1.6 ns

(*) PH24 : average of 4 pH24 measurements - REF : average of 2 measurements by the Vergé-Nicou reflectometer (a higher value indicates a paler colour) - WHC : measured by the time necessary for a piece of pH paper to become entirely wet, when applied on the freshly cut muscle.

* P < .05, ** P < .01, *** P < .001, ns P > .10

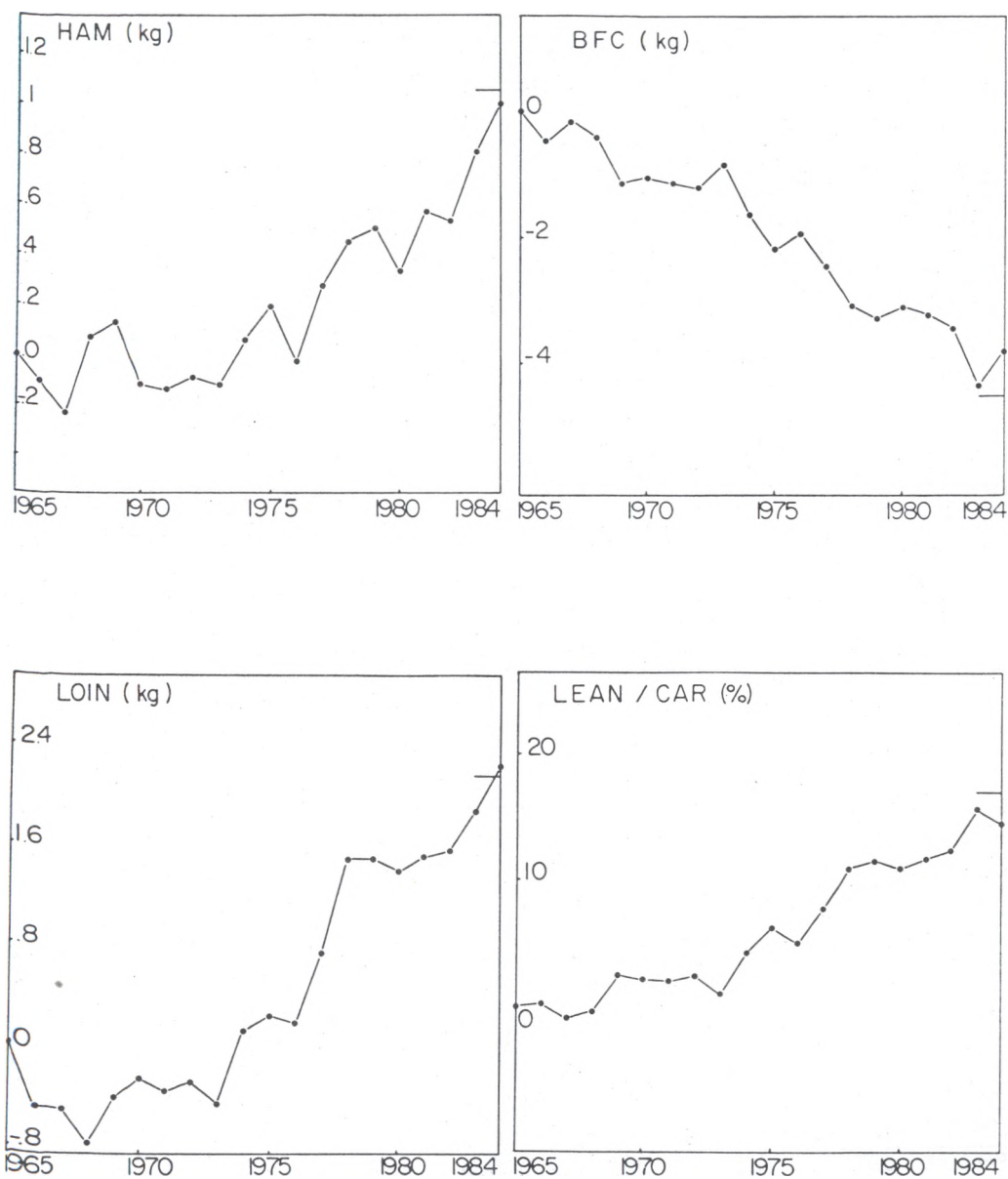


Fig. 1. Evolution of sire generations breeding values for body composition traits. HAM : weight of ham, LOIN : weight of loin, BFC : weight of backfat cut, LEAN/CAR : percentage lean in carcass (variables defined in text). Genetic level of herdbook boars indicated by a horizontal line over 1983-84.

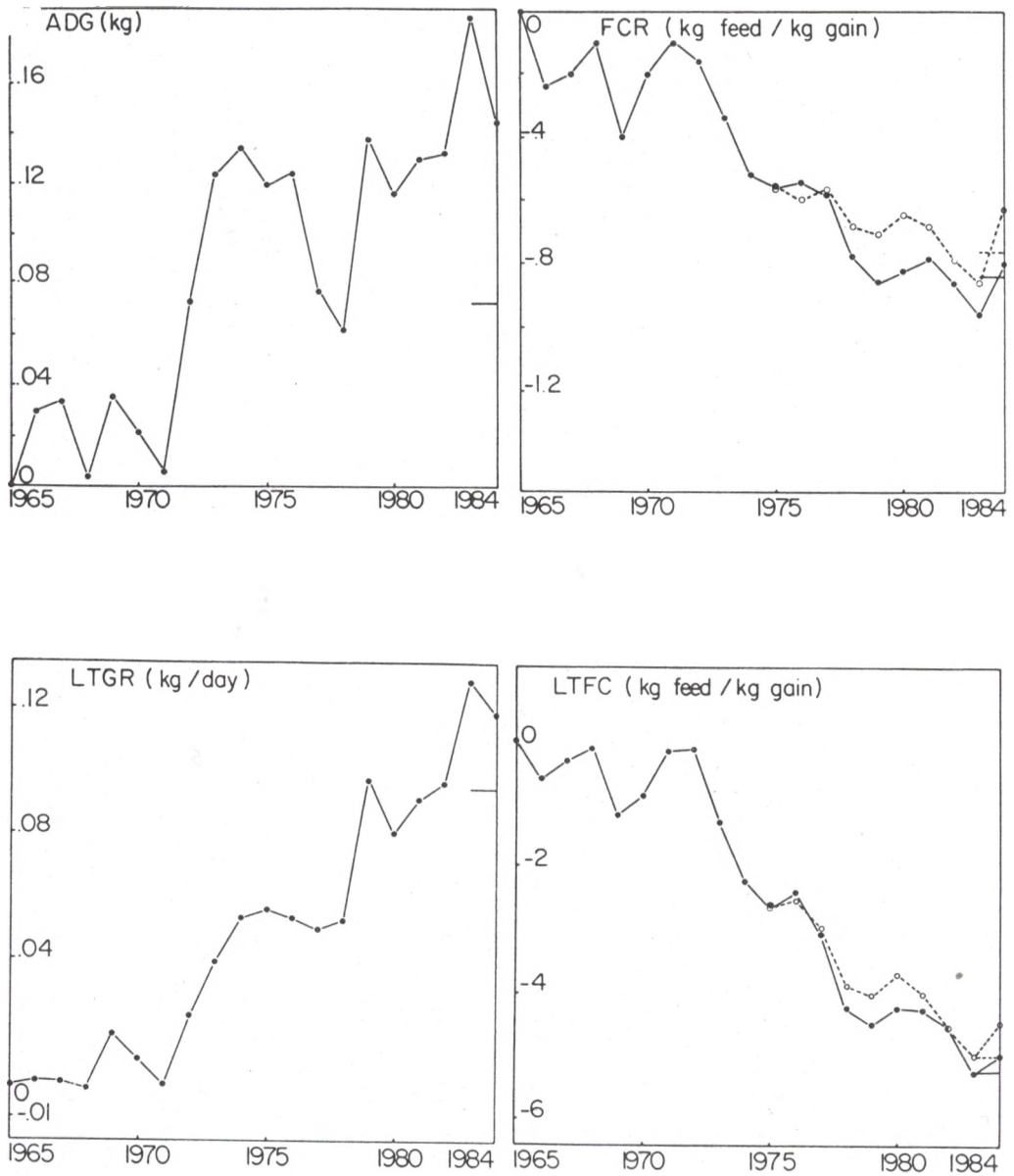


Fig. 2. Evolution of sire generations breeding values for growth and efficiency. ADG : average daily gain, LTGR : lean tissue growth rate, FCR : feed conversion ratio, solidline 30-85 kg/dotted line 30-100kg, LTFC : lean tissue feed conversion, solidline 30-85 kg/dotted line 30-100 kg (variables defined in text). Genetic level of herdbook boars indicated by a horizontal line over 1983-84.