[1] Institute of Animal Breeding and Husbandry, University Halle-Wittenberg, D-06108 Halle,
[2] Department of Animal Husbandry and Breeding, University Hohenheim, D-70593 Stuttgart

UWE WUENSCH [1], GERHARD NITTER [2] and LUTZ SCHUELER [1]

Genetic and economic evaluation of genetic improvement schemes in pigs.
1. Methodology with an application to a three-way crossbreeding scheme

Summary

A method is presented for evaluating selection strategies for a three-way cross in pigs. Multitrait selection is considered. The criteria of evaluation are the annual genetic gains in the breeding objective and its component traits, and the profit which is the net present value of return from investment in the scheme.
Selection in the sire line (Pietrain) contributes higher returns than selection in the dam lines. Meat percentage is the dominant trait in the sire line and has the highest impact on the breeding objective. The sire line is characterised by a negligible economic weight for the reproduction trait and has higher weights than dam lines for growth and carcass traits. The higher discounted economic values of these traits for Pietrain compared to those for dam lines deviate considerably from the equal weighting often applied in practical breeding programmes.

Key words: genetic and economic evaluation, selection schemes, pig, crossbreeding, performance testing

Zusammenfassung

Titel der Arbeit: **Genetische und ökonomische Beurteilung von Zuchtplänen beim Schwein. 1. Mitteilung: Methode und Anwendung für eine Dreirassenkreuzung**
Ein Verfahren für die Beurteilung von Zuchtplänen wird am Beispiel einer Dreirassenkreuzung beim Schwein vorgestellt. Die Vergleichskriterien sind die jährlichen Zuchtfortschritte der Zuchtzielmerkmale und der Züchtungsgewinn.
In der Vaterrasse (Pietrain) werden höhere Züchtungserträge erzielt als in den Mutterassen. Der Muskelfleischanteil ist das dominante Merkmal in der Vaterrasse und besitzt den größten Einfluß auf das Zuchtziel. Die Vaterrasse ist charakterisiert durch ein zu vernachlässigendes ökonomisches Gewicht für das Reproduktionsmerkmal und besitzt höhere ökonomische Gewichte für die Merkmale der Mastleistung und des Schlachtkörperwertes. Die höheren diskontierten Grenznutzen dieser Merkmale beim Pietrain im Vergleich zu den Mutterassen weichen beträchtlich von einer gleichen Gewichtung ab, wie sie häufig in Zuchtprogrammen praktiziert wird.

Schlüsselwörter: genetische und ökonomische Beurteilung, Zuchtpläne, Schwein, Kreuzungszucht, Leistungsprüfung

1.   Introduction

Genetic improvement of a population through selection is the main task of animal breeding. The aim is to select the population towards a well-defined breeding objective which suits the future production/marketing requirements of the average commercial producer. This aim should be achieved fast and be economically efficient. Thus, the criteria used to evaluate a genetic improvement scheme are the annual genetic response for the breeding objective and the profit or net return from invested money.
Applying the formula of Rendel and Robertson (1950) a large number of studies investigated how to maximize the annual genetic gain (Skjervold, 1963; Skjervold and Langholz, 1964, Nicholas and Smith, 1983). Although the basis of formulating a multitrait breeding objective

(the "aggregate genotype") had been demonstrated long before (Hazel, 1943), most of these aimed at selecting for a single trait. This holds particularly when a stochastic simulation approach rather than a deterministic procedure has been used (e.g. Ruane and Thompson, 1991). Although these studies present some basic recommendations, they are less appropriate for investigating breeding schemes in practice where the aim is usually to improve an aggregate breeding objective comprising all economically important traits.

There is still a great lack of a clear definition of the breeding objective under most circumstances. This is due to a widespread lack of cooperation between geneticists and economists. This lack of cooperation may also be the main reason why very little has been done in regard to cost/benefit analysis of breeding schemes. A methodology will be introduced which covers both evaluating the annual genetic gain for an aggregate breeding objective as well as returns and profit from the breeding scheme. For these calculations the computer program ZPLAN was used which has been developed for this purpose (Karras et al., 1993). The method is demonstrated for an example consisting of a three-way crossbreeding scheme in pigs in Saxony (Germany) with Pietrain as the sire line, and German Landrace and Large White as the dam lines. Basic assumptions about population structure, selection groups, criteria of selection and costs will be given. The aim of this paper is to present these assumptions and the results of a basic breeding scheme. These concern the distribution of the testing capacity at the central test station as well as the extent of the field test, the contribution of the breeds to both monetary genetic gain and return and the economic weights of traits in the three breeds involved. In a second paper, these assumptions will be modified in order to optimise the basic situation and simulate various testing strategies of boars in the field as well as at the central station.

2.   Material and Method

Computer program

The approch used in this study for predicting the annual genetic gain is deterministic. One round of selection is considered with its impact on a given time horizon with specific discount rates. All selection groups in the whole population are to be defined, each with a specific selection intensity and with particular sources of information for index selection including two-stage selection. The ZPLAN program applies the gene-flow method described by McClintock and Cunningham (1974), Hill (1974) and Elsen and Mocquot (1974) to calculate the number of standard discounted expressions (SDE-values) for each trait in each selection group. This is required to get both correctly discounted economic weights for the objective traits and the discounted return over the given investment period. Fixed and variable costs are assumed for certain breeding efforts and used to derive the profit which is the return minus costs. Return, cost and profit is expressed per sow in the total population. The program has been used to evaluate different genetic improvement schemes by Graser et al (1994) for beef cattle, by Riedl (1996) for dairy cattle and by Mueller (1995) and Kominakis et al. (1997) for sheep.

For this study, the three purebred lines, the F_1-sows and the terminal products are considered. Through weighting the economic values with the SDE-values, the different breeding goals for each breed involved are taken into account. Using selection index procedures the program enables the analysis of different breeding schemes for a defined investment period with respect to maximising monetary genetic gain and profit. Simulating selection strategies using different herd and population structures, testing capacities and selection intensities for performance traits, the program realises a multi-trait genetic and economic optimisation of breeding schemes. Further details are given in Nitter et al. (1994).

Population structure

The Saxonian pig breeding scheme consists of different levels in a pyramid described as nucleus, multiplier and commercial level. The breeding enterprise needs information in order to optimise mating, selection and management decisions for all breeds used in the three-way cross breeding scheme. The German Landrace breed (GL) currently consists of 4000 sows, including 800 nucleus sows and 3200 multiplier sows. The Large White breed (LW) with 100 sows is used similarly to GL as a dam line. Pietrain (Pi) with 125 sows is the sire line. The F_1-generation (LW x GL) contains 46000 sows.

	NB_GL	NS_GL	NB_LW	NS_LW	NB_Pi	NS_Pi	PS_F_1
NB_GL	1	2					
NS_GL	3	4					
NB_LW			5	6			
NS_LW			7	8			
NB_Pi					9	10	
NS_Pi					11	12	
PS_F_1		13	14				
TP					15		16

NB = nucleus boars; GL = German Landrace; NS = nucleus sows; LW = Large White; PS = production sows; Pi = Pietrain; F_1 = F_1-generation (LW x GL); TP = terminal products (Pi (LW x GL)); > = produce; 1, 5, 9 = nucleus boars > nucleus boars; 2, 6, 10 = nucleus sows > nucleus boars; 3, 7, 11 = nucleus boars > nucleus sows; 4, 8, 12 = nucleus sows > nucleus sows; 13 = nucleus sows > production sows; 14 = nucleus boars > production sows; 15 = nucleus boars > terminal products; 16 = production sows > terminal products

Fig.: Transmission matrix of the three-way cross with 16 selection groups. Origin of parents (gene donors) in columns, offspring (gene recipients) in rows (Übertragungsmatrix der Dreiwegekreuzung mit 16 Selektionsgruppen. Abstammung der Eltern (Genspender) in den Spalten, der Nachkommen (Genempfänger) in den Reihen)

Selection groups

Figure shows the 16 selection groups in the transmission matrix of the gene flow method described by Hill (1974) and Elsen and Mocquot (1974). Twelve selection groups are defined in the nucleus units, where boar selection occurs both to improve boars (boars to breed boars, NB>NB) and females (boars to breed sows, NB>NS). Selection of females in the nucleus also intends to improve boars (sows to breed boars, NS>NB) and females (sows to breed sows, NS>NS). These groups describe the four-path model used and are reflected in the three purebred blocks (GL 1-4, LW 4-8, Pi 9-12). In figure 1 is also clearly shown that nucleus sows of GL (NS>PS, 13) produce the production sows (e.g. F_1-generation of sows) after mating with LW-sires (NB>PS, 14). No reciprocal crossing is assumed. The F_1-sows (PS>TP, 16) again generate the terminal products (e.g. slaughter pigs) after mating with the terminal Pietrain sires (NB>TP, 15).

Table 1
Sources of information for selection in various selection groups and selection steps (Informationsquellen für die Selektion der verschiedenen Selektionsgruppen und Selektionsstufen)

Selection group	Genetic group	Information source	Field / Station	No. of animals	No. of litters	Recorded traits
Boars, 1st selection step	all	Ind, F, FF	F	1		ADG, US
		M	F	1	1	NBA, ADG, US
		FM	F	1	3	NBA, ADG, US
		FS F	S	2		DG, LMP, FE, pH_1
	GL	HS F	F	60	1	NBA
	LW, Pi	HS F	F	10	1	NBA
	all	HS F	S	calc.‡		DG, LMP, FE, pH_1
	GL	HS M	F	60	1	NBA
	LW, Pi	HS M	F	10	1	NBA
	all	HS M	S	calc.		DG, LMP, FE, pH_1
	all	HS Ind	S	calc.		DG, LMP, FE, pH_1
Boars, 2nd selection step†	GL	Progeny	S	calc.		DG, LMP, FE, pH_1
	LW_P	Progeny	S	calc.		DG, LMP, FE, pH_1
	LW_C	Progeny	F	calc.		LMP, pH_1, ADG
	Pi_P	Progeny	S	calc.		DG, LMP, FE, pH_1
	Pi_C	Progeny	F	calc.		LMP, pH_1, ADG
Gilts, 1st selection step	all	Ind	F	1		ADG, US
		F, FF	F	1		ADG, US
		M	F	1	1	NBA, ADG, US
		MM	F	1	3	NBA, ADG, US
Sows, 2nd selection step†	all	Ind	F	1	1	NBA

† additional to information of first selection step; ‡ calculated; Ind = self performance; F = father; FF = father's father; M = mother; FM = father's mother; FS F = full sib's of father; HS F = half sib's of father; HS M = half sib's of mother; HS Ind = half sib's of proband (paternal); DG = daily gain (test period); NBA = number of piglets born alive; LMP = meat percentage; ADG = average daily gain (life time); FE = feed efficiency; US = ultrasonic side-fat thickness; pH_1 = pH-value (45 min.); GL = German Landrace; LW = Large White; Pi = Pietrain; LW_P = Large White boars mated with Large White sows; LW_C = Large White boars mated with German Landrace sows to produce the F_1-generation; Pi_P = Pietrain boars mated with Pietrain sows; Pi_C = Pietrain boars mated with F_1-generation to produce the terminal products

Selection criteria

Sources of information for selection in the different selection groups are shown in Table 1. Within a breed, they are identical for boars in the first stage, independent of the kind of later use for mating (purebred or crossbred). The number of relatives assumed to have records in the various selection groups depends on parameters such as boar to sow ratio, survival rates and data recording. This explains that in GL more recordings are available for selection than in the other two lines.

Selection at the nucleus level for production as well as for reproductive traits takes place in two stages. In the first step, the animals are selected upon data from the performance test of the animal itself and its ancestors with additional full- and half-sib information. In a second selection step the best boars in the self-performance test are progeny tested at the station (purebred matings) and in the field (crossbred matings) to select the boars for replacement of the nucleus boars. Boars serving merely to produce crossbreds are tested only in the field. At the station a boar is tested with 4 progeny groups. Each group consists of 2 piglets per litter of the same sex (male in GL, females in LW and Pi). The animals are kept in group housing and the feed efficiency is measured individually. For testing under field conditions, the group size is assumed to consist of 6 slaughtered animals per successful mating. The evaluation takes

place with completion of the progeny test. For sows, the number of piglets born alive (NBA) in the first litter is the criterion in the second selection stage.

In Table 2, the selection criteria are listed with their phenotypic standard deviations, heritabilities and phenotypic/genetic correlations. Standard deviations differ between dam and sire lines according to recent findings in Saxony (Mueller, pers. comm., 1997). Furthermore, for the five traits included in the breeding objective, the non-discounted economic values derived on commercial level are shown. They have been calculated as the difference between the additional revenue and additional costs from increasing the trait by one unit and were referred to one piglet basis.

Table 2
Traits and their non-discounted economic values (v), heritabilities (h^2), phenotypic standard deviations (σ_P) and phenotypic and genetic correlations (phenotypic correlations above and genetic correlations below the diagonal) (Merkmale und ihre undiskontierten Grenznutzen (v), Heritabilitäten (h^2), phänotypische Standardabweichungen (σ_P) und phänotypische und genetische Korrelationen (phänotypische Korrelationen oberhalb, genetische Korrelationen unterhalb der Diagonale)) †

Trait	Unit	h^2	σ_P		v	Genetic and phenotypic correlations						
			GL, LW	Pi	DM	DG	LMP	FE	pH_1	NBA	ADG	US
DG	g/d	.35	95	85	.11	-	-.15	-.55	-.15	0	.40	.20
LMP	%	.55	2.2	2.3	4.5	-.20	-	-.15	-.30	0	0	-.30
FE	kg/kg	.35	.24	.16	-36	-.65	-.20	-	.05	0	-.20	0
pH_1	.1	.20	.20	.18	2.0	-.25	-.35	.05	-	0	-.15	.10
NBA	piglets	.10	2.0	1.7	7.5	.10	0	0	0	-	0	0
ADG	g/d	.20	45	50	-	.50	0	-.30	-.20	.05	-	0
US	mm	.25	.15	.12	-	.30	-.40	.20	.10	0	.15	-

† for abbreviations, see footnote Table 1

In order to use purebred and crossbred information for estimating the breeding value of purebred sires, a connectedness is to establish for the traits measured on progeny tested animals at station and for those tested in the field (Mueller and Mielenz, 1986). Because correlations of the same trait in pure- and crossbreeding progeny are not unity, they have to be considered as two traits. Assumed correlations are given in Table 3 derived on the basis of estimations of Brandt (1994). Newer results received more attention in which relationships between animals were considered in detail and more animals were involved. Correlations of different traits between pure- and crossbreds were derived according to the model of path coefficients (Wright, 1934) as published estimates are mainly related to correlations of the same trait. Resulting genetic and phenotypic matrices were checked with the computer program MATDEF (Mielenz and Wagenknecht, 1992) to ensure that they were positive definite. In case of non-positiveness the program determines a positive definite matrix which has a minimum distance to a given non-positive matrix. This procedure makes it possible to include information of the progeny test in the field for the selection of purebred boars.

Table 3

Genetic correlations used between purebred and crossbred information (Verwendete genetische Korrelationen zwischen Reinzucht- und Kreuzungsleistungen)

Traits	Large White - F_1			Pietrain - end product
	Variant 1	Variant 2	Variant 3	Variant 4
DG	-	-	0.8	-
LMP	-	0.7	0.9	0.7
FE	-	-	0.6	-
pH_1	-	0.7	0.9	0.7
NBA	0.6	-	-	-
ADG	0.7	0.7	0.7	0.7
US	0.8	-	0.8	-

Variant 1: Large White self performance in the field to F_1 self performance in the field; variant 2: Large White progeny (purebred) at the station to Large White progeny (crossbred) in the field; variant 3: Large White progeny (purebred) at the station to Large White progeny (crossbred) at the station; variant 4: Pietrain progeny (purebred) at the station to Pietrain progeny (crossbred) in the field

Biological and technological parameters

In Table 4 biological and technological parameters are listed for the basic situation. Usual lengths of productive lifetime for boars and sows in the different levels were assumed. To compare productive lifetimes, attention has to be paid to the time for the first use of boars and sows for matings. Table 4 shows that boars after the self-performance test at an age of 11 months (1st selection step) are already used to breed purebred sows and crossbreds. After the completion of the progeny test at an age of 22 months (2nd selection step) they breed purebred boars after being mated with progeny tested sows (planned matings). Planned matings are also assumed for sows to produce boars. In the multiplier and the production levels a very wide boar to sow ratio is assumed due to the high percentage of artificial inseminations in Saxony. This circumstance enables higher selection intensity for boars used to produce crossbreds. Furthermore, a reduction of selection intensity occurs because 15 % of the boars are not suitable for artificial insemination and an additional 20 % do not survive until completion of the progeny test. Finally, 20 % of selected gilts are also not available for breeding because of no pregnancy.

Table 4

Biological and technological parameters for the basic situation (Biologische und technologische Parameter der Ausgangssituation)

Age of animal when first litter is born (months)	Selection step	
	First	Second
Boar sires	-	22
Sow sires	11	-
Boar dams	-	17
Sow dams	11	-
Productive lifetime (months)		
Boar sires	-	12
Sow sires in the nucleus unit	11	12
Sow sires in the multiplier level	11	18
Sow sires in the production level	11	24
Boar dams	-	14
Sow dams in the nucleus unit	6	14
Sow dams in the multiplier level	6	18
Sow dams in the commercial level	36	-
Boar to sow ratio		
Purebreds - German Landrace	1 : 40	
- Large White	1 : 20	
- Pietrain	1 : 20	
Multiplier level	1 : 160	
Commercial level	1 : 330	
Survival and reproduction		
Time between births (months)	5.5	
Self performance tested boars (number per year)		
- German Landrace	80	
- Large White	70	
- Pietrain	200	
Losses of boars during self performance test at station (%)	25	
Boars suitable for artificial insemination (%)	85	
Losses of boars until completed progeny test (%)	20	
Rate of pregnancy (%)	80	

Investment parameters and costs

Investment parameters and costs are necessary to take the economic side of the breeding programme into account. Changing the investment parameters would have an effect on the SDE-values and thus on return, because they also affect the economic weights of traits in the breeding objective. Variable and fixed costs, however, affect neither returns nor genetic response. But investment parameters and costs both influence the profit. The investment parameters used as well as fixed and variable costs are shown in Table 5. Not included are costs occurring in the usual production process regardless of the recording scheme. Fixed costs include overhead costs to maintain the breeding programme. Variable costs are costs directly related to performance and pedigree recording. They are multiplied by the number of animals incurring these costs and occur mainly in the nucleus unit. Also shown in Table 5 is the time of occurrence of variable cost, which has to be taken into account.

Table 5
Investment parameters and costs (Investitionsparameter und Kosten)

Investment parameters		
Investment period (years)	10	
Interest rate for returns (%)	6	
Interest rate for costs (%)	4	
Fixed and variable breeding costs (DM)		
Fixed costs per year	420 750.-	
Progeny test of boars - per sow and litter	30.-	(.3)†
- per piglet	7.50	(.3)
Station test per animal	130.-	(.4)
Slaughtering an animal at station	35.-	(.6)
Self performance test of an animal in the field	12.-	(.6)
Breeding performance test per sow	20.-	(1.)
Additional costs for a purchased boar from outside the breeding area	1500.-	(.6)
Proportional costs for housing a boar during the progeny test		
at the station	600.-	(1.4)

† average time of occurrence (in years), i.e. the difference between the time of birth of selected animals and the time of occurrence.

3.   Results and discussion

Distribution of the test station capacity

Table 6 shows the distribution of the testing capacity for various genetic groups in the breeding scheme. The figures are obtained by varying the number of tested boars under a given number of tested groups per boar and tested animals per group with respect to maximise the profit. For evaluating young boars in the self-performance test, information from tested full- and half-sibs at station are taken into account. The GL breed claims the highest proportion of the capacity of the central test station with 43 percent through 36 tested boars. In Pietrain, nearly 31 boars and in LW approximately 17 boars should be tested per year. The small number of station tested animals in LW is also due to the decreased selection intensity in sow selection, because female piglets tested on station are lost for breeding. As expected, Pietrain boars require the highest proportion of testing capacity in the field (75 % compared to 25 % for LW boars). This is attributable to the number of Pietrain boars needed for mating F_1 sows and the more than 14 times lower quantity of LW boar matings with GL sows to produce the F_1 generation.

Genetic gains and returns

Table 7 demonstrates the different natural and monetary genetic gains and the contributions to the return of the three lines in this crossbreeding scheme. The trait NBA has a considerably higher genetic gain in the dam lines (.075 piglets in GL and .072 piglets in LW) than in the Pietrain breed (-.006 piglets). LW and Pietrain are superior in traits related to fattening performance and carcass quality traits. The main difference between these two lines is in LMP, for which Pietrain is superior with an annual genetic gain of .495 versus .303 percentage points in LW. This emphasises its position as a sire line. The differences in the mean generation interval for purebred animals are very small. The higher monetary genetic gain in LW and Pietrain in spite of the small population size is explained by the inclusion of information from crossbred offspring in the evaluation of nucleus boars.

Table 6
Number of tested boars per year and tested animals per boar in station and field test as well as distribution of testing capacity after optimisation in number of testing boars (Anzahl getesteter Eber je Jahr und getesteter Tiere je Eber auf der Station und im Feld sowie die Verteilung der Testkapazität nach der Optimierung der Anzahl an Testeber)

	GL	LW	Pi	LW_C	Pi_C
	Station	Station	Station	Field	Field
Number of boars tested	36	17	31	26	79
Animals per boar †	8 (4)	8 (4)	8 (4)	60 (10)	60 (10)
Number of tested animals	288	136	248	1560	4740
Tested animals in percent within station and field	43	20	37	25	75

LW_C = Large White boars mated with German Landrace sows to produce the F_1-generation; Pi_C = Pietrain boars mated with F_1-generation to produce the terminal products; † tested groups per boar in brackets

Table 7
Natural and monetary genetic gain per year, generation interval, return, costs and profit (Naturaler und monetärer Zuchtfortschritt je Jahr, Generationsintervall, Züchtungsertrag, Züchtungskosten und Züchtungsgewinn) †

Parameter	Unit	GL	LW	Pi	Total
Natural genetic gain per year					
DG	g	11.07	12.54	12.75	
LMP	%	0.183	0.303	0.495	
FE	kg/kg	-0.030	-0.039	-0.033	
pH_1	.1	-0.012	-0.012	-0.015	
NBA	piglets	0.075	0.072	-0.006	
ADG	g	6.48	5.34	6.72	
US	mm	-0.0024	-0.0018	-0.009	
Mean generation interval	years	1.82	1.83	1.81	1.82
Monetary genetic gain per year	DM	3.66	4.65	4.74	4.35
Return for single traits					
DG	DM	1.65	1.36	3.52	6.53
LMP	DM	1.02	1.67	6.31	9.00
FE	DM	1.38	1.39	3.00	5.77
pH_1	DM	-.03	-.03	-.09	-.15
NBA	DM	1.46	1.25	-.01	2.70
Return, total	DM	5.48	5.64	12.73	23.85
Return, percent	%	23	24	53	
Costs, total	DM				12.83
Profit	DM				11.02

† For abbreviations of traits, see footnote Table 1

The three traits DG, LMP and FE contribute most to the total return. The returns in Pietrain are more than two times higher for DG and FE, and LMP is even more than three times superior than in the dam lines. For this reason, Pietrain contributes at a rate of more than 50 percent to the total return of 23.85 DM per sow in the investment period. In the dam lines, the returns are relatively balanced between most of the traits. The trait pH_1 has a very small and negative contribution to the return. After subtraction of the costs, the breeding scheme leads to a profit of 11.02 DM per sow.

Economic weights

Non-discounted economic values of the traits (shown in Table 2) were multiplied by the standardised discounted expressions (SDE-values) of the selection groups in the nucleus and averaged over the selection groups in a line. The resulting discounted economic values, using DG in GL as a reference point, are presented in Table 8. These clearly show that the sire line is characterised by a negligible value for NBA, because reproductive performance is realised only by a restricted number of purebred sows. On the other hand, fattening performance and carcass quality traits are expressed in a high number of crossbred descendants, so that for those traits the sire line obtains higher values than the dam lines.

The relative economic weights reflect the relative economic importance of each trait within a line. They were calculated through weighting the discounted economic values with the genetic standard deviation, summing up the results of a line and expressing them in percent. The weight of LMP is higher in the sire line than in the dam lines (39.2 % versus 27.8 and 25.1 % resp.), whereas the weight of NBA in the dam lines is high (29.4 and 35.8 %).

Table 8
Discounted economic values and relative economic weights of traits in the breeding goal for the breeds (Diskontierte Grenznutzen und relative ökonomische Gewichte der Zuchtzielmerkmale der Rassen)

Trait †	Discounted economic values (DM/unit)			Relative economic weights (%)		
	GL	LW	Pi	GL	LW	Pi
DG (g/d)	0.11	0.06	0.19	23.3	21.5	33.2
LMP (%)	4.52	2.53	7.89	27.8	25.1	39.2
FE (kg/kg)	-35.17	-19.66	-61.37	18.8	17.0	26.5
pH_1 (.1)	2.01	1.12	3.51	0.7	0.6	0.9
NBA (piglets)	12.38	9.31	0.09	29.4	35.8	0.2

† For abbreviations of traits, see footnote Table 1

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Authors addresses
Dr. UWE WÜNSCH
Kirchberger Str. 41
D-08107 Cunersdorf
uwuensch@t-online.de

Dr. GERHARD NITTER
Institut für Tierhaltung und Tierzüchtung der
Universität Hohenheim
Garbenstraße 17
D-70599 Stuttgart

Prof. Dr. LUTZ SCHÜLER
Institut für Tierzüchtung und Tierhaltung der
Martin-Luther-Universität Halle-Wittenberg
Adam-Kuckhoff-Str. 35
D-06108 Halle (Saale)