FEED-A-GENE

Adapting the feed, the animal and the feeding techniques to improve the efficiency and sustainability of monogastric livestock production systems

Deliverable D5.5

Demonstration of the use of social effects and crossbred and genomic information to improve selection and feed efficiency

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1. Summary

Objectives: The rate of improvement in feed efficiency in Europe is, time and again, lower than it could be. Increases in slaughter weight, non-castration, feed prices, and other factors obscure the trend. This does not mean that all these factors have a negative impact on feed efficiency. Non-castration for example improves feed efficiency. In this deliverable we studied if (1) understanding group dynamics can help to increase rate of improvement (it hardly does) and (2) if adding field data (i.e., crossbred data, via the use of genomics) to data collected on selection candidates can help to increase accuracy of selection (it does). Information collected on purebred animals has partially, for largely unknown reasons, a different genetic background, which can be captured by proper modelling and the use of genomics.

Rationale: Most livestock animals are kept in groups. The group dynamics can lead to damaging behavior and can, more subtle, also positively influence performance parameters. There is very good evidence that genetic variation in indirect genetic effects exists, and that it can be validated in masked data. Attempts to show added value in a commercial environment are mostly unsuccessful. A novel approach, relating feed intake data to social ranking shows promise, especially since this feed intake data is available on a large scale. Another novel approach, the analysis of culled rearing gilts because of damage on ears or tails, shows considerable genetic variation.

The application of the crossbred genomic toolset on protein deposition in crossbred finishers yielded a high/low contrast in which clear differences in nitrogen efficiency were shown. This is a proof of principle valuable for a different definition of feed efficiency, not in terms of energy, but in terms of protein or nitrogen.

In conclusion, the genetic and genomic toolset is continuously improving and focusing more and more on the final product. Social interactions are important for behavior, can be statistically described, and have a genetic background. Improvement in feed efficiency will come, for now, more from the physiological than from the behavioral side. Genomic prediction of production traits is improving each year and predicts future performance of young animals better and better.

Teams involved: Topigs Norsvin, Wageningen University & Research

Species and production systems considered: The results were demonstrated on pigs, but they should also be valid in similar contexts for other monogastric species. The relative costs of the different options should, however, be specifically evaluated before application in these other productions.

2. Introduction

The general objective to improve selection for feed efficiency on monogastric animals is to achieve more accurate estimated breeding values (**EBV**) of crossbred production animals while selecting purebreds in nucleus farms. To do so, multiple angles have been explored in the first years of the Feed-a-Gene project, including recording new types of traits, using genomic information, using information collected on crossbred, and accounting for new factors in the genetic models, including heritable genetic social effects of the pen mates (or indirect genetic effects, **IGE**) on animal's traits. Ultimately, models were used to test new features. A specific task was dedicated to the further validation of some of these effects. Specific data were produced to nourish the developments and decision making for selection strategies, to validate the importance and use of social effects and crossbred data for improving selection for feed efficiency.

The concepts explored in the previous project tasks (e.g., deliverable D5.4) were demonstrated, including an empirical demonstration of the computation of genomic indexes for selecting purebred animals for crossbred performance in pigs. Large groups of crossbred offspring tested for feed efficiency and production traits have been individually genotyped with a low-density SNP chip in the three first years of the project (1000/year). These allow computing the Genomic Breeding Values (GEBV's) of their genotyped parents with classical pedigree-based EBV's to predict the average outcome of their crossbred offspring. Genotyped crossbred offspring gives the opportunity to account for breed effects in GEBV computations. The validation of the GEBV accuracy was applied to feed efficiency traits but also to social interaction skills of the animals, by creating social and less social pens.

In this document the three following specific objectives are reported:

1. *A validation of the use of GEBV's for crossbreds, based on a dataset created in Feed-a-Gene.* Knowledge obtained from the project on how to use commercial data in genetic evaluation programs was applied to sort animals for grouping in different experiments of different ambitions. First an experiment was carried out on protein efficiency to validate the selection potential. The same genetics were also used in the larger experiment for selection of indirect genetic effects.
2. *The results of trials designed to better understand the underlying mechanisms of the animal's social interaction skills.* Results of trials executed before and during the start of Feed-a-Gene (being not part of the project) have been inconclusive. These trials will be briefly discussed. Learning from these trials and the knowledge from the validations, we executed a high/low trial on indirect genetic effects for average daily gain (**ADG**) within the project;
3. *Results from the dataset created within the project to validate the new models for feed efficiency.*

3. Results

3.1 Genomics for crossbreds works!

One of the objectives was to validate the use of GEBV's for selection for crossbred performance. In this section, the results of three different trials are described that show the added value of the use of GEBV's for crossbreds. One trial is based on a dataset created for this genetic project. Another trial concerned a protein metabolism study, and the last trial was a pilot trial performed at Schothorst Feed Research, of which the data was also used as a training dataset for the High/Low experiment described in section 3.4.

3.1.1 Grouping pigs based on genomics

We first aimed to validate the potential of crossbred genomics to improve the accuracy of predicting performance of individual crossbred pigs. To do so, two batches of crossbred pigs were genotyped, and the pigs were divided in four groups based on their genomic estimated breeding value (GEBV) and pig performance was measured.

3.1.1.1 Material and methods

Pigs used in this study originated from a three-way cross (i.e., synthetic boar x (Large White x Landrace) sow. The experiment was executed in two batches. Per batch, piglets of 16 sows were genotyped, resulting in approximately 200 piglets being genotyped per batch. The genotype of the piglets was used to estimate GEBV's for crossbred performance of every pig. Based on the GEBV's for average daily gain, individual average daily feed intake (**ADFI**), backfat thickness (**BF**), loin depth (**LD**) and the measured birth weight (**BiW**), an index was calculated. In the index, these five traits were weighed according to their economic values. Feed efficiency itself was not part of the index, but since its underlying traits ADG and ADFI were part of the index, weighed according to their economic weight, feed conversion ratio (feed:gain or **FCR**) was indirectly included.

At the start of the grower-finisher period, the animals were divided into four (GEBV-) groups based on the index: high, mid-high, mid-low, and low. The GEBV-groups and boars and gilts were housed separately. For each batch, two compartments were used with eight pens each, leading to a total of 16 pens per batch including two pens per sex and GEBV-group.

The grower-finisher phase started on average at 25.3 kg at approximately 66 days of age. The pigs were kept in the facilities until they reached a slaughter live weight of approximately 120 kg. Each pig was allowed a minimal space of 1 m². Floors of the pens were 60% concrete and 40% slatted. The pigs had *ad libitum* access to feed throughout their life. They were fed a commercial starter diet from day 0 to day 25 in test, a commercial grower diet from day 26 to day 67, and a commercial finisher diet from day 68 until slaughter weight.

In both batches, pigs were weighted at day 0, day 56, and at the end of the study (day 104 ± 6.7). The backfat measurements were recorded at day 56 and at the end of the trial using an ultrasound instrument (Renco Lean Meater; Renco Corp., Minneapolis, USA). The ADG was calculated as the difference between body weight measurements divided by the timespan between the measurements. In the first batch, daily feed intake was registered based on pen level, and the ADFI per pen was calculated as the cumulated daily feed intake per pen (corrected for number of animals per pen) divided by the timespan over which feed intake records were collected. Pen FCR was calculated as the ratio between ADFI on pen level and

mean ADG of the pigs in a pen. For the second batch, the experimental facilities (Schothorst Feed Research BV) were equipped with IVOG feeding stations (INSENTEC, Marknesse, The Netherlands) that register individual feed intake of group-housed pigs. All pigs had ear tags with unique numbering. Individual feed intake records were therefore available for all pigs for each day on test. The ADFI was calculated as the cumulated individual daily feed intake records divided by the timespan over which the feed intake records were collected, whereas the FCR was calculated as the ratio between individual ADFI and individual ADG.

3.1.1.2 GEBV calculation

For calculating GEBV's over the last 6 years, data of about 1,900,000 purebred and 600,000 (F2) crossbred animals were available. For all animals, at least live-time daily gain measurements were available. The trait with the least number of observations, ADFI, still contained data on 170,000 purebred and 19,000 crossbred animals. The pedigree contained about 2,800,000 animals of which 340,000 were genotyped (i.e., 320,000 purebreds and 20,000 crossbreds). The genotyped animals were used to create a genomic relationship matrix applying APY (Misztal *et al.*, 2015). Both the traditional relationship matrix based on the pedigree and the genomic relationship matrix were blended to create a joint relationship matrix, the so-called H^{-1}. The latter is used in breeding value estimations.

Breeding values were estimated using MiXBLUP (Ten Napel *et al.*, 2018). The genotyped piglets without any phenotype were added to the pedigree so MiXBLUP provided estimates for them as well. All phenotypes were split into two different traits: one for purebreds and one for crossbreds. The GEBV for the crossbred traits were used in this experiment to sort animals based on the selection index in GEBV-groups, as described above.

3.1.1.3 Results

There was a clear difference between GEBV groups in Start BW, ADG, backfat thickness, lean meat percentage, and days in test (Table 1). In addition, ADFI and FCR were different between the GEBV groups for pigs measured on the individual level, but on the pen level this effect was not present. For FCR, the pattern of group results resembled those of individual results, except that they were not as significant (P=0.09). The ADG was not analyzed as pen average because in both batches, individual ADG was recorded and analyzed. Animals with a higher GEBV index compared to a low GEBV index were 5 kg heavier at start of the experiment, grew 44 g/day more, consumed 100 g/d less feed, had a 0.2 point lower FCR, were 2 mm leaner, had 1.3% more lean meat, and took 7 days less to reach slaughter weight. There was no difference between the groups in loin depth and mortality.

Table 1. Least squares means estimates of grower-finisher performance of pigs grouped based on their genomic estimated breeding value (GEBV) for an index based on average daily gain (ADG), average daily feed intake (ADFI), back fat thickness (BF), loin depth (LD) and the measured birth weight (BiW). Results of ADFI, and feed conversion ratio (FCR) are based on individual measurements (n=165) and pen averages (n=16).

Trait	GEBV group				*P*-value					
	High	Mid High	Mid Low	Low	Group	Sex	BiW	Start BW	HCW	Batch
Individual										
Start BW (kg)	27.4^{a}	26.2^{b}	25.1^{b}	22.5^{c}	<.001	0.254	-	-	-	<.001
ADG (g/d)	966^{a}	937^{bc}	958^{ab}	921^{c}	0.017	<.001	0.025		-	<.001
ADFI (kg/d)	2.26^{ab}	2.20^{a}	2.31^{bc}	2.39^{c}	<.001	0.137	-	<.001	-	-
FCR (g/g)	2.24^{a}	2.27^{a}	2.34^{b}	2.44^{c}	<.001	<.001	-	<.001	-	-
BF (mm)	12.1^{a}	12.1^{a}	13.1^{b}	14.1^{c}	<.001	0.155	-	-	<.001	0.008
LD (mm)	64.1	63.7	62.8	63.1	0.381	0.001	-	-	<.001	0.001
LM (%)	60.3^{a}	60.3^{a}	59.6^{b}	58.9^{c}	<.001	0.219	-	-	<.001	0.016
Days in test (d)	98^{a}	102^{b}	102^{b}	105^{c}	<.001	0.006	-	-		<.001
Mortality (%)	3.7	0.3	6.0	2.5	0.132	-	-	-	-	0.043
Pen										
ADFI (kg/d)	2.31	2.29	2.33	2.25	0.344	0.262	-	0.291	-	-
FCR	2.44	2.47	2.50	2.58	0.091	0.005	-	0.374	-	-

BW, body weight, LM, lean meat, HCW, hot carcass weight.
^{a,b} Values within a row with different superscripts differ significantly at $P < 0.05$.

3.1.1.4 Conclusion

This experiment showed that crossbred genomics can be used to predict the grower-finisher performance of crossbred pigs in commercial environments.

3.1.2 High/Low protein deposition predicts nitrogen efficiency

Following this positive outcome, the effects of the genetic capacity to deposit protein on fecal N-digestibility, N-retention, and N-efficiency of crossbred pigs were tested. Crossbred pigs were genotyped, divided the pigs in two groups based on their genomic estimated breeding value for protein deposition (GEBV-PD), and a nitrogen balance (N) study was performed in individual pigs. Although the underlying dataset is different, the technique used to estimate the GEBV-PD is identical to the one described in section 3.1.1.2. The data has been made available and described in deliverable D2.4.

3.1.2.1 Materials and methods

The study was conducted to evaluate the effects of birth weight and genetic capacity to deposit protein on N-retention and N-efficiency in pigs using two levels of dietary protein supply (adequate and restricted; 100 and 70%, respectively). Each animal was subjected to both dietary regimes. Piglets were born at the Swine Innovation Centre Sterksel of Wageningen UR (The Netherlands) and 100 of them were genotyped. The genotyped piglets were pre-selected for birth weight (50 high/50 low extremes). The genotypes of the piglets were used to estimate genomics-based breeding value for protein deposition (GEBV-PD) of each individual pig. At 4 weeks of age, the piglets were weaned and at 9 weeks of age piglets were moved to the barn for growing-finishing pigs. At 14 weeks (98 days of age), 40 male pigs (20 high; 20 low) were preselected considering birth weight, litter origin, and GEBV for protein deposition. These pigs were transported to the experimental facilities of Wageningen University in Wageningen. Upon arrival (day 0), pigs were housed individually in metabolism cages and allowed to adjust to the housing conditions for a period of one week (experimental day 0-7). The experimental diets were provided from day 7-11, before the first balance period in which feces and urine were

collected quantitatively (day 12-17). The animals then received the other diet (day 17-23) before carrying out a second N-balance study (day 23-28). During the experimental periods, the pigs fed the protein adequate diets were fed at a feeding level of 2.8 times the maintenance energy requirement. The pigs on the protein-restricted regime received the same amount of energy-supplying ingredients relative to their metabolic body weight ($BW^{0.75}$), but with a 30% restriction in the amount of protein supplied via the diet. This was achieved by restricting the supply of each of the dietary protein sources to a level of 70% relative to the supply in the protein-adequate regime. Drinking water was available *ad libitum*.

3.1.2.2 Results

The difference in GEBV-PD between the high and low groups was 13.2 g/d, with the low GEBV-PD pigs having a value of -2.3 g/d and the high GEBV-PD pigs 10.8 g/d, based on an average protein deposition of 146 g/d for the crossbred pigs. Birth weight, weight at start of the experiment, and weight at end of the experiment was not different between the high and low GEBV-PD pigs. The N-intake and N-feces in g/kg $BW^{0.75}$/day was not different between high and low GEBV-PD pigs (Table 2).The N-urine (g/ kg $BW^{0.75}$/day) was higher in the low GEBV-PD pigs and N retention (g/ kg $BW^{0.75}$/day) was higher in the high GEBV-PD pigs when fed the diet with adequate protein, but there was no difference between the GEBV-PD pigs on the restricted diet (Table 2). The N-efficiency, measured in % of N consumed retained in the body, was 5% higher in the high GEBV-PD pigs when fed the diet providing adequate protein, and 1.1% higher when fed the diet restricted in protein (not significantly different).

Table 2. Effect of genomic estimated breeding value (GEBV) of protein deposition (Low vs High) and dietary protein supply (adequate versus restricted) on nitrogen (N) intake, N-excretion via feces and urine, and total N retention. ns=not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Adequate Diet		Restricted Diet		*P*-value		
	Low	High	Low	High	GEBV	Diet	GEBV x Diet
N intake, g/kg $BW^{0.75}$/day	2.20		1.61		ns	***	ns
Fecal N, g/kg $BW^{0.75}$/day	0.17				ns	ns	ns
Urinary N, g/kg $BW^{0.75}$/day	0.94	0.82	0.54	0.54	*	***	**
N retention, g/kg $BW^{0.75}$/day	1.10	1.21	0.89	0.91	*	***	*
N efficiency, %	50.2	55.2	55.2	56.3	*	**	*

3.1.2.3 Conclusion

This experiment showed that crossbred genomic information can be used to estimate the protein deposition of crossbred grower-finisher pigs, as animals with a higher GEBV-PD had a lower urinary nitrogen excretion, a higher nitrogen retention and a higher nitrogen efficiency.

3.1.3 Genetic correlations for crossbred traits

Deliverable D5.4 was about the use of commercial data in a pig breeding program. Knowledge on genetic correlations, especially the purebred-crossbred correlations, are decisive for the design of a genetic evaluation targeting the improvement of crossbred performance. Table 3 summarizes these estimates.

Table 3. Genetic correlations amongst purebred and crossbred grower finisher traits (from Aldridge *et al.*, 2019; deliverable D5.4).

	FCR_pb	IG_ADG_cb	IG_ADG_pb	ADG_cb	ADG_pb	DFI_cb	DFI_pb
FCR_cb	0.57	-0.70	-0.20	-0.70	-0.20	0.73	-0.03
FCR_pb		-0.11	-0.68	-0.12	-0.68	0.32	0.61
IG_ADG_cb			0.4	1.00	0.40	0.93	0.04
IG_ADG_pb				0.40	1.00	0.03	0.04
ADG_cb					0.51	0.93	0.04
ADG_pb						0.02	0.76
DFI_cb							0.54

FCR_cb = Feed conversion ratio crossbreds (DFI_cb/ADG_cb); FCR_pb = Feed conversion ratio purebreds(DFI_cb/ADG_cb); IG_ADG_cb = Individual average daily gain crossbreds (ADG_cb with an indirect genetic effect fitted); IG_ADG_pb = Individual average daily gain purebreds (ADG_pb with an indirect genetic effect fitted); ADG_cb = Individual average daily gain crossbreds (Total average daily gain); ADG_pb = Individual average daily gain purebreds (Total average daily gain); DFI_cb = Individual daily feed intake crossbreds (Total daily feed intake); DFI_pb = Individual daily feed intake purebreds (Total daily feed intake).

Research reported in deliverable D5.4 (Table 3) showed that the purebred-crossbred correlations are low, which implies that for optimum use of commercial data, purebred- and crossbred traits should be treated as different traits. Below a threshold of 0.8, it is considered favorable to split traits in purebred and crossbred variants. Feed conversion ratio and all other traits connected to feed efficiency examined here showed levels below this threshold. This is especially true for the indirect genetic effects for daily gain. The purebred-crossbred correlation was 0.4, which is lower than usually reported. This might be one of the explanations for disappointing results on the high/low trials on IGE for ADG so far (see section 3.2). The study of Aldridge *et al.* (2019) also yielded the variance components for usage in a genetic evaluation.

The dataset was quite unique since it contained a large number of pedigreed grower-finishers with individual recording of average daily gain and feed intake and thus feed efficiency, all originating from one sire line of which the sires had simultaneously purebred- and crossbred offspring. A substantial part of the (purebred and crossbred) animals was genotyped. Nevertheless, for some traits it was difficult to estimate the purebred-crossbred correlation, probably because no animal has both a purebred and crossbred trait. While we show, and others have too, that the genetic correlation is lower than expected between purebreds and crossbreds, there is reason to continue this line of research as it has practical implications for the industry. If we can find ways to improve these estimates, it could result in more accurate breeding values and faster rate of progress.

3.2 Indirect Genetic Effects and selection

Indirect genetic effects (IGEs) are heritable effects of an individual on trait values of another individual, and are a result of social interactions. IGEs are estimated together with the direct genetic effect (DGEs), which represents the heritable effect of an individual on its own performance. Obviously, to estimate IGE's it should be known which animals were grouped together during performance test. To accurately estimate the IGE, an additional fixed effect (i.e., compartment) and two additional random effects (i.e., pen and compartment within contemporary group) should be added to the statistical model while estimating breeding values. One phenotype of each animal within the pen is used to estimate the breeding values for IGE and DGE.

An animal's total breeding value for the trait is then calculated as DGE + n.IGE; where n = pen size-1. A number of studies were run before Feed-a-Gene, or in complementary projects. A summary of these studies and of their main teachings will be described here, that served as the basis for the developments to account for social interactions proposed in Feed-a-Gene, presented in parts 3.3 and 3.4.

3.2.1 First variance components estimations

The first studies on the heritability of indirect genetic effects in pigs date back to 2008. Bergsma *et al.* (2008) reported heritable genetic variance for the indirect genetic effects on average daily gain and daily feed intake, but not on body composition traits and residual feed intake (Table 4). At that time, no studies were performed to understand the mechanisms underlying the phenomenon of indirect genetic effects, but a potential for improvement of efficiency related traits was identified.

Table 4. Genetic parameters, heritability (h^2), common environmental effects (c^2), group effects (g^2), and compartment within contemporary group effects (f^2) for growing-finishing traits (from Bergsma *et al.* 2008).

	Model*	h^2 / T^2 †	c^2	g^2	f^2	σ^2_A / σ^2_{TBV} †
Daily gain, g/d‡	1	0.24	0.04	0.11	0.17	1,843 ± 148
	2	0.34	0.04	0.09	0.16	2,654 ± 346
Net daily gain, g/d§	1	0.22	0.04	0.11	0.17	1,473 ± 118
	2	0.32	0.04	0.10	0.16	2,117 ± 279
Ultrasonic back fat, mm	1	0.38	0.03	0.05	0.10	1.48 ± 0.14
Carcass back fat, mm	1	0.38	0.03	0.03	0.03	2.53 ± 0.38
Carcass muscle depth, mm	1	0.24	0.02	0.02	0.03	7.21 ± 0.56
Feed intake, g/d	1	0.19	0.03	0.20	0.27	13,324 ± 1,647
	2	0.35	0.03	0.17	0.25	24,568 ± 6,326
Residual feed intake, g/d	1	0.11	0.04	0.21	0.25	3,883 ± 723

* Model 1: Animal model without social effects, Model 2: Animal model including heritable social effects.
† Heritability (h^2) was replaced by the proportion of the heritable variance compared to phenotypic variance (T^2) and the additive genetic variance (σ^2_A) was replaced by the σ^2_{TBV} when Model 2 was used. See Bijma *et al*. (2007a and 2007b) for derivation of formulas. Pen size (n) of 8.5 and average relatedness within pens (r) of 0.18 was used;
‡ Based on live weight.
§ Based on hot carcass weight (used to estimate live weight).

3.2.2 High/Low selection experiment at WUR

One of the first experiments trying to understand the mechanisms behind indirect genetic effects (IGE) was executed as part of the doctoral study of Irene Camerlink at Wageningen University (2014).

3.2.2.1 Material and Methods

The objective was to determine the consequences of selection for IGEs for average daily gain (IGE_{ADG}) on the behavioral repertoire of pigs in a set-up dedicated to detection of genotype by environment interactions. One generation of selection was applied to create a high vs. low IGE_{ADG} contrast in 480 pigs (4-23 weeks of age) housed in barren and straw-enriched pens (n = 80 pens with 6 pigs per pen).

3.2.2.2 Results

Pigs already showed tail damage from the moment of weaning, with an average tail damage score of 2.2 (Figure 1). During the nursery phase (week 4 – 7), there was no difference between the IGE_{ADG} groups for tail damage (P = 0.93), but a clear difference was present between

barren and enriched pens (tail damage score nursery: barren 2.3 ± 0.04; enriched 1.8 ± 0.04; $P < 0.001$). During the finishing phase (week 8 – 23), high IGE_{ADG} pigs had a lower tail damage score (high 2.0 ± 0.05; low 2.2 ± 0.05; $P = 0.004$), and the positive effect of enrichment remained (mean tail damage score finishing: barren 2.6 ± 0.05; enriched 1.6 ± 0.05; $P < 0.001$). This resulted in an additive effect of IGE_{ADG} group and straw enrichment on tail damage, without interactions between these two factors ($P = 0.79$).

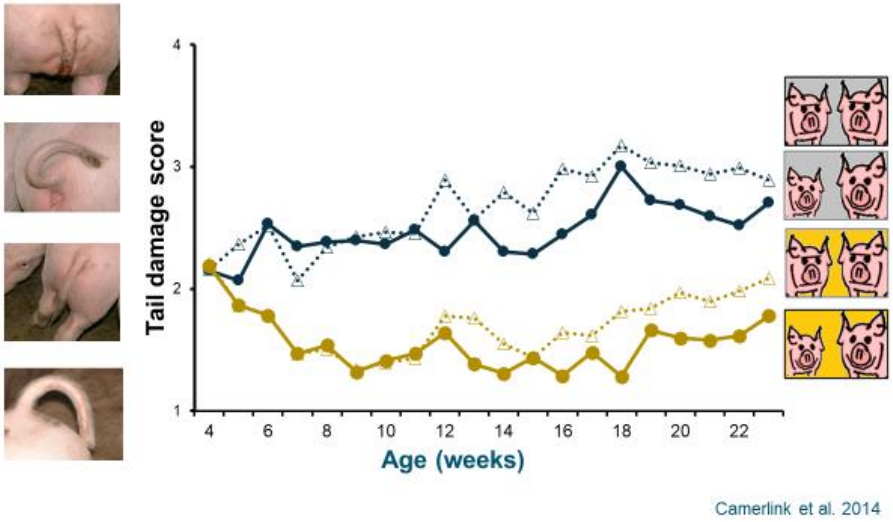

Figure 1. Tail damage depending on high (solid lines) or low (dotted lines) IGE_{ADG} groups and housing (blue grey = barren pens; yellow = straw enriched pens). Tail damage score 1 being no visible tail damage; score 2 for hair removed from the tail; score 3 for bite marks; and score 4 for a clearly visible wound.

3.2.2.3 Conclusions

In conclusion, selection on high IGE_{ADG} reduced potentially harmful biting behaviors in pigs. However, average daily gain was not significantly affected.

Given that most pig husbandry in the pork production chain does not always fully fulfill the natural needs of the pig, this can result in shortage of nutritional elements and/or frustration, leading to tail biting. The majority of farmers has reacted with tail docking and (fewer) with teeth clipping. Larger farms, fewer workers, and a forthcoming ban on tail docking make understanding tail biting more urgent. Management practices need attention, and genetic selection might favor the animals that fits best their environment. Behavior is difficult to score. While consequences of damaging behaviors (e.g., bitten tails, scratches) can easily be used to find victims, it is more difficult to find biters. The same holds for mortality. From these and the previously presented results, (damaging) behavior is likely to be a social interaction trait, as the actions and activities of a pig not only depend on the pig itself, but also depend on the behavior and actions of its pen mates. Literature suggests that there is a genetic component involved, since some breeds have a higher incidence of damaging behavior (e.g., tail biting) than others (Penny and Hill, 1974; Fraser and Broom, 1997; Schrøder-Petersen and Simonsen, 2001; Breuer *et al*., 2003). Altogether, we conclude that to maximize the response to selection for behavior, both direct and indirect genetic effects (IGE) should be accounted for.

3.2.3 Validation of Indirect Genetic Effects for average daily gain

The study of Camerlink *et al*. (2014) did not show a significant difference in average daily gain between the high EBV IGE_{ADG} -groups and the low EBV IGE_{ADG} -groups. These results do not rule out the possibility that findings of Bergsma *et al*. (2008) were an artefact. Obviously, if one would like to include IGE for ADG in a breeding program, it is important that IGE is for real. Moreover, it helps in understanding the mechanisms behind indirect genetic effects. Therefore, Duijvesteijn (2014) performed a formal validation of these effects during her PhD. The validation of IGE being delicate because of low heritability, and thus low reliability of EBV's (Table 5).

Table 5. Variance components for average daily gain (ADG), without and with indirect genetic effects (IGE) in the model.

Item	Without IGE_{ADG}	With IGE_{ADG}
σ^2_{DGE}	2893	2762
$covar_{DGE,IGE}$		27
σ^2_{IGE}		13
σ^2_{group}	1270	1121
$\sigma 2_{farm\text{-}comp\text{-}c.group}$	2249	2013
σ^2_{common}	603	606
$\sigma^2_{full\ Sib}$	661	660
σ^2_{error}	5966	6047
h^2/T^2	0.21	0.35
r_g		0.14
σ^2_P	13643	13339
σ^2_{TBV}		4641
LogL	-9126	-9121

DGE = direct genetic effect; IGE = indirect genetic effect.

To run the validation study, variance components were estimated from 107,626 animals from two purebred sire lines and five farms, all born between 2002 and 2015. Only sires with more than 80 offspring (415 sires) were kept. The last 20% offspring of these sires that were performance-tested were used for validation, by removing their phenotype and those of all their "farm-compartment-contemporary group" mates. The breeding values (DGE and IGE) of these 14,664 offspring animals were predicted from the remaining data included in the training data set. Finally, the obtained breeding values were correlated with the original pig phenotypes to evaluate the prediction accuracy with and without IGE (Table 6).

Table 6. General correlations with corrected phenotypes for average daily gain.

	Correlation with phenotype
Direct genetic effect from classical model	0.328
Direct genetic effect from IGE model	0.327
Sum of IGE of j pen mates	0.219
Predicted phenotype from IGE model	0.352

Including indirect genetic effects for ADG provided a slightly higher correlation with the phenotypes than the classical model (0.352 versus 0.328). The total genetic variance increased substantially by accounting for IGE (4641 versus 2893), as did the heritability (Table 5), and the genetic correlation between direct- and indirect genetic effects was slightly positive (0.14), so no antagonistic effects is anticipated between the two components. It can thus be

concluded that including indirect genetic effects in genetic evaluations improves the reliability of estimated breeding values in a formal validation for ADG.

3.2.4 Modelling IGE: current work on tail biting

This study, run from September to December 2019 during the MSc Internship of Iris van den Broek at Wageningen University, aimed to identify the opportunities to reduce stress and mortality during finishing and during transport of pigs using indicator traits related to traces of cannibalism and aggressions among pigs.

3.2.4.1 Material and methods

Data on culling (e.g., for damaging behavior) was available from the Topigs Norsvin rearing facilities for breeding gilts in Germany. A total of 15,941 pigs from three different rearing farms were scored, just before the animals were moved to clients with piglet producing farms. If the animal was unsuited to sell and had to be culled, the reason for culling was recorded. The breeding gilts were loaded on a truck at the farm of birth as one group per shipment, unloaded at the rearing farm, and subsequently penned in order of unloading. Thereby, pen composition during rearing is regarded as random.

Double records of an animal were removed (both), resulting in a database with 15,826 pigs. Next, a unique group number was generated for pigs that were in the same pen during the same period of time, with pen being the physical unit and group being the temporary combination of animals in that pen. This group number was based on the farm, month and year of testing, and the pen number. On all three facilities, the majority of the pen size was 12 animals per pen. In total 1,504 groups were identified. Body weight (average 88.4kg) and age at weight recording (average 145.1 d) were known as well.

For estimating genetic parameters, the pedigree-file contain 20,344 animals. The statistical model used for both ADG and skin damage was:

$$Y_{ijklmn} = \mu + FARM_i + YYYYMM\text{-}TEST_j + PEN_k + \underline{ANIMAL_l} + \underline{PENMATE1..15_m} + \underline{GROUP_n} + \underline{e_{ijklmn}}$$

Where Y_{ijklmn} is the average daily gain or skin damage (0/1) of animal *l*, $FARM_i$ is the effect of farm *i* on animal *l* (*i* = 1 to 3), $YYYYMM\text{-}TEST_j$ is the effect of the j^{th} year-month of test on animal *l* (*j* = 1 to 38), PEN_k is the effect of k^{th} physical location within $FARM_j$ on animal *l* (*k* = 1 to 1,360), $ANIMAL_l$ is the (random) direct effect of the l^{th} animal (*l* = 1 to 15,826), $PENMATE_m$ is the (random) indirect effect of the m^{th} penmate on animal *l* (*m* = 1 to 15,826 and $m \neq l$), $GROUP_n$ is the (random) effect of the n^{th} contemporary group formed by a pen within date of testing on animal *l* (*n* = 1 to 1,504), e_{ijklmn} is the residual effect of animal *l* reared at farm *i* in YYYYMM-test *j* penned in PEN *k* together with $PENMATE_m$.

3.2.4.2 Results

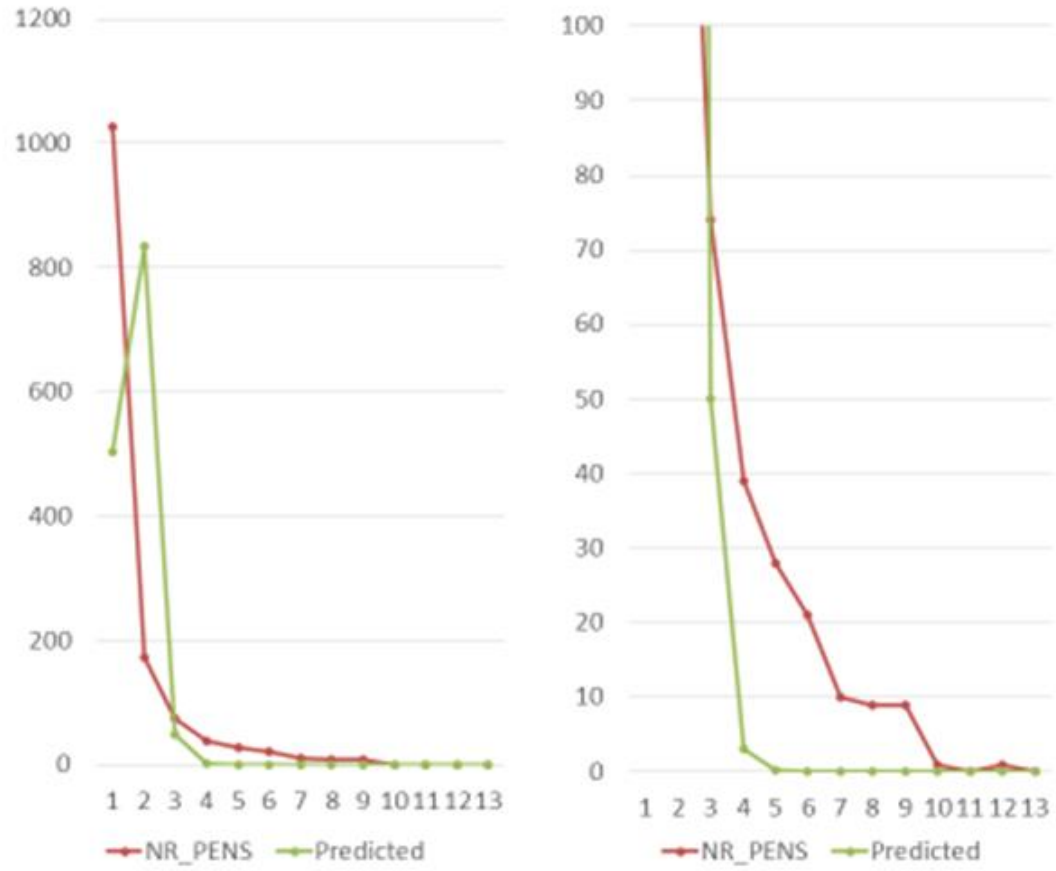

Figure 2. Frequency of damaging behavior (cannibalism). Frequency on the Y-axis and number of damaged animals on the X-axis with a pen size of 12. The red line represents the number of pens observed and the green line represents the number of expected pens given the frequency of 6%. The right panel zooms in on the pens with three or more damaged pigs, and indicates that the number of pens with 4-9 skin damaged pigs outnumber the expected number of pens based on the observed frequency. This could be considered as an indication for the presence of a culprit.

Table 7. Overview of variance components, the proportion of total genetic variance relative to the total phenotypic variance (T^2 or h^2), and the genetic correlation between indirect (A_I) and direct (A_D) genetic effects (r) for Model 1 and Model 2 for the trait cannibalism.

		Model 1		Model 2
	Symbol	Including IGE	Excluding IGE	Including IGE
Direct genetic variance	$\sigma^2_{A_D}$	28.78	29.72	29.40
Indirect genetic variance	$\sigma^2_{A_I}$	1.37	-	0.75
Direct-indirect covariance	$\sigma_{A_{DI}}$	-1.09	-	-0.70
Group variance	σ^2_{group}	98.35	112.6	88.78
Body weight variance	σ^2_{weight}	-	-	0.00
Age variance	σ^2_{age}	-	-	0.02
Residual variance	σ^2_e	395.08	397.08	395.72
Total genetic variance	$\sigma^2_{A_T}$	128.24	29.72	81.70
Total phenotypic variance	σ^2_P	535.02	539.4	520.89
T^2 or h^2	T^2 or h^2	0.24	0.06	0.16
Genetic correlation	$r_{A_{DI}}$	-0.17	-	-0.15
Akaike Information Criterion		-29180.09	-29166.79	-27771.42
Relative likelihood		1	0.0013	0.0

The heritable variance for skin damage with the model including IGE was 24%. This value exceeds the usual heritabilities for this trait, indicating that social effects captures additional heritable variance (Breuer *et al*., 2005; Hermesch and Guy, 2019; Canario and Flatres-Grall, 2018). With $h^2 = 0.06$ and $T^2 = 0.24$, the total heritable variance is four times greater than direct additive genetic variance, meaning that social effects contribute to 75% of the heritable variance. These results show that social effects contribute largely to the heritable variance in skin damage in this population. The increase in heritability is in the range of values found by other studies when accounting for this component (Bijma *et al*., 2007b; Bergsma *et al*., 2008; Ellen *et al*., 2008; Canario and Flatres-Grall, 2018; Peeters, 2015). Being a victim or being the cause does seem to be genetically two different traits. The genetic correlation between the direct effect (being skin damaged) and the indirect genetic effect (causing the skin damage) is, although negative, low and not significantly different from zero (standard errors are not given here).

No heritable variance was found for lifetime daily gain, not in a model with a direct genetic effect only, nor in a model with both the direct genetic and indirect genetic effect. Data originated from rearing facilities where animals are fed restricted. This might be the explanation for a lacking heritable variance. Unfortunately, this also means that we were not able to estimate the genetic correlations between (damaging) behavior and daily gain.

3.2.4.3 Conclusions

In conclusion, it is possible to estimate genetic parameters on skin damage in pigs for direct as well as indirect effects. From model comparisons based on Akaike Information Criterion, it can be concluded that model 1a, including indirect genetic effects, is the best model. Even though pen effects appeared to be significant, including these in the model did not result in a better fit. In addition, as pen effect was significant and part of the total variance can be explained by the group variance, it is suggested that physical differences between the pen (e.g., ventilation, enrichment, and space allowance) could potentially influence the incidence of tail biting and are easier to change on the short term if factors are identified.

3.3 Novel traits for improving feed efficiency

Given the difficulty to capture and show selection effects of IGE predictions on production traits, alternative strategies based on the use of automatic feeder records were tested in the project.

3.3.1 Feed behavior traits

This study was run by Sanne Hermans as part of her minor thesis (The effects of feed intake behavior on feed efficiency in pigs) in Animal Breeding and Genetics at Wageningen University in January, 2018.

3.3.1.1 Introduction

The objective of this study was to develop an additional behavioral trait that can be used in breeding programs to improve feed efficiency by capturing social interactions. A prerequisite of this trait was that it should be measured with registrations of a feeding station, because it has to be easily measurable. First, genetic parameters for feed intake behavior traits were estimated. Subsequently, a rank index was made based on the registrations of the electronic feeding stations. Phenotypic and genetic parameters for the rank and the feed intake behavior traits were estimated.

3.3.1.2 Material and methods

For the genetic analysis of the feed intake behavioral traits, information from feeding stations from five different farms were used: three nucleus farms and two commercial farrow-to-finish farms. The number of pens equipped with an electronic feeding station (EFS) ranged from 40 to 130 per farm. On the nucleus farms data on one purebred sire line was used only. The crossbred grower-finishers on the commercial farms were sired by the same sire line.

After data editing, data of 37,034 individuals were available. These animals were penned together in 4,214 groups. Of these animals, feed intake characteristics of 2,265,000 days were used. Nearly 80% of the individuals were purebreds. The remainder were crossbreds from three different commercial sow crosses. The pedigree contained 46,870 animals.

3.3.1.3 Behavior traits

In Table 8 the heritabilities for different traits are given, ranging from low (visiting time) to moderate (number of visits and number of meals) heritabilities.

Table 8. Heritabilities ($h^2 \pm SE$) and variance components for the company-compartment-start-date combination (σ^2_{CCS}), pen-start-date combination (σ^2_{PS}), litter (σ^2_{Li}), animal (σ^2_A), and residual (σ^2_E).

Trait	h^2	σ^2_{CCS}	σ^2_{PS}	σ^2_{Li}	σ^2_A	σ^2_E
Feeding rate (g/min per day)	0.14 ± *0.01*	225	10	23	73	208
Nr. of visits (per day)	0.26 ± *0.01*	11.3	15.5	10.6	14.3	92.4
Visiting time (min. per day)	0.10 ± *0.01*	212.7	5.6	7.8	30.5	56.4
Nr. of meals (per day)	0.30 ± *0.02*	2.5	2.1	2.1	2.6	17.4
Meals time (min. per day)	0.10 ± *0.01*	201.5	6.8	7.7	29.4	55.7

Table 9 shows the results of the additive genetic correlations between the different dependent variables. Genetic correlations ranged between -0.63 and 0.78. The daily feed intake was highly and positively correlated with growth (0.78), feed conversion ratio (0.63) and back fat thickness (0.63).

The feeding rate is the result of the feed intake divided by the meals time, so the amount of feed an animal consumes per minute per day. This explains the positive correlation with the daily feed intake (0.48), the higher the feed intake, the higher the feeding rate. It also explains the negative correlation with the meals time (-0.63), the higher the feeding time, the lower the feeding rate. The backfat thickness of the pigs was moderately correlated with the feeding rate, daily feed intake, growth and feed conversion ratio. The table shows that the feed conversion ratio was positively correlated with the feeding rate (0.51), and lowly with the other feeding traits.

Table 9. Estimates of genetic correlations (r_g ± *SE*) for production traits and feed intake behavior traits.

Trait	Average daily gain	FCR	Back fat	Feeding rate	N° of visits	Visiting time	N° of meals	Meals time
Daily feed intake	0.78 *±0.02*	0.63 *±0.03*	0.63 *±0.03*	0.48 *±0.04*	0.08 *±0.04*	0.14 *±0.05*	-0.01 *±0.04*	0.14 *±0.05*
Average daily gain		-0.03 *±0.06*	0.37 *±0.04*	0.24 *±0.05*	-0.04 *±0.05*	0.23 *±0.05*	0.01 *±0.05*	0.24 *±0.05*
FCR			0.51 *±0.04*	0.51 *±0.05*	0.10 *±0.05*	-0.09 *±0.05*	-0.02 *±0.05*	-0.09 *±0.05*
Backfat thickness				0.46 *±0.04*	0.01 *±0.04*	-0.04 *±0.04*	-0.05 *±0.04*	-0.03 *±0.04*
Feeding rate					-0.01 *±0.05*	-0.63 *±0.03*	0.01 *±0.05*	-0.63 *±0.03*
N° of visits						0.05 *±0.04*	0.82 *0.01*	0.06 *±0.04*
Visiting time							-0.03 *±0.04*	N.C.*
N° of meals								-0.04 0.04

*N.C. indicates that the genetic parameter estimations did not converge.

3.3.1.4 Rank index

Based on data from the electronic feeders, one can determine which animal chased another animal away while visiting the feeder. The animal chased away is recorded as a loss, and the one chasing the other animal away is recorded as a win. The animal with the highest ratio of wins to losses is considered the most dominant animal. In this way, the hierarchy within a pen is determined, ranging from 1 (the most dominant animal) to the number of pen mates (the most docile animal), called the Blom's rank score (Puppe *et al*., 2008). The Blom's score will be interpreted as high for docile animals (i.e., low rank), and low for dominant animals (i.e., high rank). Some first indications about this criterion were also provided in deliverable D5.2 of the project.

3.3.1.5 Phenotypic parameters

Table 10 shows the results of the average values of the traits for the different groups. The first group consists of the most dominant individuals (20%). These animals had the highest ratio of number of wins to number of losses. The feed intake per meal and feed intake time per meal was for the first group lower than for the other groups. The averages of these two traits increased for the second group and were the highest for the group with the 20% most docile animals. The average feed conversion ratio was the highest for the dominant individuals and the lowest for the docile individuals, so the latter had the best feed conversion ratio. The

average daily gain was 23 gram lower for the docile individuals compared to the dominant individuals.

Table 10. Mean values (± *SE*) for feed intake behavior traits for high (dominant), middle (average) and low ranked (docile) animals according to Blom's rank index.

	Ranking		
	20% high (dominant)	60% middle (average)	20% low (docile)
Number of animals (#)	3222	9518	3151
Number of wins (#)	472	375	264
Number of losses (#)	354	383	371
Number of visits ± SD (#)	22.4 ± *14.0*	20.2 ± *13.8*	18.3 ± *12.4*
Feed intake per meal ± SD (g)	232 ± *117*	252 ± *122*	269 ± *130*
Time per meal ± SD (min)	4.63 ± *2.77*	5.18 ± *2.99*	5.52 ± *3.06*
Feeding rate ± SD (g/min/d)	56.8 ± *25.7*	54.8 ± *24.1*	54.8 ± *26.7*
Feed conversion ratio ± SD (g/g)	2.29 ± *0.39*	2.25 ± *0.38*	2.24 ± *0.38*
Average daily gain ± SD (g/d)	1039 ± *145*	1028 ± *144*	1016 ± *140*

3.3.1.6 Genetic parameters

The heritability for the rank index was 0.12 (SE ± 0.02). Table 11 shows the results of the genetic correlations of feed related traits with the rank Blom-score, which ranged between -0.15 and 0.43. The rank index was positively correlated with the daily feed intake, so that feed intake of docile individuals (high rank Blom-score) is higher in comparison to the dominant individuals. The negative genetic correlation with the number of visits confirmed the phenotypic result that dominant individuals (i.e., individuals with a lower Blom-score) have a higher visiting rate. The positive correlation for the feed intake per meal and feed intake time per meal confirmed the phenotypic result that docile individuals had a higher feed intake and feed intake time per meal.

Table 11. Genetic correlation for Blom's rank index (± *SE*).

	Daily feed intake	Number of visits	Feed intake per meal	Feed intake time per meal	Feeding rate	FCR	Average daily gain
Rank Blom-score	0.39 *± 0.08*	-0.15 *± 0.08*	0.20 *± 0.07*	0.21 *± 0.08*	0.13 *± 0.10*	0.26 *± 0.09*	0.43 *± 0.08*

3.3.1.7 Conclusions

The aim of this study was to develop an additional behavioral trait, which can be used in breeding programs to improve the feed efficiency while accounting for social interactions. The genetic parameters for the feed intake behavior of the fattening period were estimated on basis of registrations of electronic feeding stations. Heritabilities ranged from 0.10 (visiting time and meals time) to 0.38 (back fat thickness). The genetic correlations with feed efficiency ranged from -0.63 (feeding rate and meals time) to 0.78 (daily feed intake and average daily gain).

From the phenotypic analyses, it appeared that the most dominant individuals had the lowest feed intake per meal, and time per meal, and the highest average daily gain. The most docile individuals had the best feed conversion ratio and highest feeding rate. Finally, the genetic parameters for the rank index were calculated. The heritability for Blom's rank score was 0.12. Although, none of the phenotypic correlations were significant in a formal sense, the genetic

correlations did not confirm the results of the phenotypic analyses for all traits. Daily feed intake (not shown in Table 10), feeding rate, feed conversion ratio, and average daily gain showed a different direction compared to what the phenotypic results suggest. The genetic correlation for number of visits, feed intake per meal and time per meal coincides with the phenotypic trend.

In conclusion, data from electronic feeding stations can be used to make a rank index, which can be included in the breeding program to improve the feed efficiency. This type of approach might be easier to implement in a breeding program than systematic estimations of IGE to account for social interactions. However, this information is only available for animals fed using electronic feeders with no door isolating the animal during a visit. This is a limited part of breeding programs, compared to growth rate measurements that are available for most individuals.

3.4 High-Low IGE_{ADG} experiment

Despite repeated research on the underlying mechanisms of heritable indirect genetic effects, no irrefutable proof of gains for selection was found. Results suggest that animals with a high genetic merit for the indirect genetic effect for average daily gain show less damaging behavior (e.g., by tail biting). Damaging behavior itself seems subjected to indirect genetic effects, which allows us to distinguish between the victim and the aggressor. No study is known to the authors that estimated genetic correlations between the indirect genetic effect for ADG and the direct or indirect genetic effect for damaging behavior. The latter could serve as ultimate proof of the mechanism behind the indirect genetic effect for ADG. That was the rationale for performing a large experiment within this project to apply “for real” knowledge on crossbred genomics to maximize differences while creating a high IGE-group and a low IGE-group. By executing such an experiment the selection effect on pig performance can be observed and correlations can be quantified.

3.4.1 Materials and methods

The first part of the trial (i.e., creating a training dataset) was done at the commercial farrow-to-finish farm of Kerrsies-Spreeuwenberg in Mantinge, the Netherlands. Grower-finishers were a three-way cross from one sire line and a commercial F1 sow. Two different F1 sows were used, both Landrace x Large White crosses, but with different types of Landrace. All grower-finishers were genotyped.

The actual high/low-experiment was performed at the Schothorst Feed Research farm in Lelystad, the Netherlands. This is a 350-sow farrow-to-finish unit. The grower-finishers on this farm were also a three-way cross from one sire line and a commercial F1 sow. The sire line is the same as the one used on the Kerssies-Spreeuwenberg farm. Three different F1 sows were used. Two Landrace x Large White-crosses and one Large White x Large White-cross. The Landrace x Large White-sows are the same as the F1-sows on the Kerssies-Spreeuwenberg farm, and there are no reasons to believe that the results would be affected by the type of crossbreds. Schothorst Feed Research produces on average ± 50 litters every three weeks. Liveborn piglets from the top 10 and bottom 10 litters on GEBV IGE_{ADG} from parental information were genotyped, in total 250 to 300 piglets every three weeks. The GEBVs (including the piglet’s own genotype) were available from the nursery phase onwards. From these piglets, the 48 piglets with highest GEBV and the 48 piglets with the lowest GEBV were housed in the grower-finisher facilities, with 12 pigs per pen. Animals were penned depending

on sex, genetic group (high/low), and start weight. Start weight was used to create uniform pens within sex and genetic group. By doing so we created a 2 by 2 factorial trial (2 sexes and 2 IGE_{ADG}-levels). One compartment contained eight pens, meaning that one compartment was used every three weeks.

The data recording protocol was similar on both farms. Individual feed intake was recorded using electronic feeders. Body weight of animals was measured at start of the growing finishing phase and at the day before slaughter. During the last four weeks of the finishing phase on both farms, a standardized diet with at least 2.5% lignin as a (biological) marker was fed to the animals. The diet differed between farms though.

Three different models were used for the statistical analyses:

$$Y_l = \mu + HIGHLOW_l + e_l \quad [1]$$

$$Y_{ijkl} = \mu + SEXE_i + LINE_j + BATCH_k + b_1BWT + HIGHLOW_l + e_{ijkl} \quad [2]$$

$$Y_{ijkl} = \mu + SEXE_i + LINE_j + BATCH_k + b_1BWT + b_2WT + HIGHLOW_l + e_{ijkl} \quad [3]$$

where Y_{ijkl} is the phenotypic observation (see Table 12), $SEXE_i$ is the effect of sexe *i* (gilt/boar) on highlow-class *l* (*i*=1 to 2), $LINE_j$ is the effect of line *j* on highlow-class *l* (*j*=1 to 3), $BATCH_k$ is the effect of the k^{th} year-week on-test on highlow-class *l* (*k*=1 to 9), BWT is the effect of the co-variable birth weight, WT is the effect of either the co-variable off-test weight (ultrasonic backfat), hot carcass weight (backfat carcass, loin depth carcass, meat-% and dressing-%) or on-test weight (feed intake), $HIGHLOW_l$ is the effect of the l^{th} EBV-group (high/Low) based on the GEBV-IGE_{ADG} at birth (*l*=1 to 2), and e_{ijkl} is the residual effect of sexe *i* of line *j* put on-test in batch *k* with highlow-group*l*.

3.4.1 Results & discussion

The Least Squares Means of the high/low trial on GEBV-IGE_{ADG} are given in Table 12.

Table 12. Least Squares Means of grower-finisher performance of pigs grouped based on their genomic estimated breeding value (GEBV) for the indirect genetic effect on average daily gain (ADG) (N=634).

	Trait	Model	GEBV IGE_{ADG} group*		*P*-value
			High	Low	
Nº of animals	(#)		312	322	
	GEBV IGE_{ADG} at birth (g/d)	1	35.2	-31.1	<0.0001
	GEBV DGE_{ADG} at birth (g/d)	1	49.2	47.1	0.6014
	GEBV IGE_{ADG} at off test (g/d)	1	11.0	-16.7	<0.0001
	GEBV DGE_{ADG} at off test (g/d)	1	43.7	50.4	0.0463
Measurements	Birth weight (kg)	1	1.38	1.36	0.4331
	Weaning weight (kg)	2	7.2	7.2	0.8495
	On test weight (kg)	2	23.1	23.0	0.5846
	Mid test weight (kg)	2	66.0	67.6	0.0226
	Off test weight (kg)	2	128.6	130.5	0.0164
	Ultrasonic backfat (mm)	3	11.3	11.4	0.2185
	Daily feed intake (kg/d)	5	2233	2295	0.0004
	Hot carcass weight (kg)	2	97.4	98.5	0.0622
	Backfat carcass (mm)	4	13.8	14.2	0.0480
	Loin depth carcass (mm)	4	67.9	68.2	0.5409
	Meat carcass (%)	4	59.2	59.0	0.0510
	Dressing percentage (%)	4	76.1	75.9	0.3941
	Mortality (%)	-	-	-	
Calculated traits	On test variation (kg)	-	3.1	3.0	
	Off test variation (kg)	-	12.3	12.1	
	Days in test (d)	-	113.9	112.3	
	Average daily gain (g/d)	2	964	988	0.0044
	Feed Conversion Ratio (g/g)	2	2.33	2.33	0.9928
	Protein deposition (g/d)	2	164	168	0.0195
	Lipid deposition (g/d)	2	183	191	0.0065
	Residual Feed Intake (g/d)	2	-66	-64	0.8796
	Protein digestibility (%)	-	-	-	
	Crude Fiber digestibility (%)	-	-	-	
Feed behavior	Nº of meals (#/d)	2	27.5	28.0	0.5434
	Nº of visits (#/d)	2	30.3	30.4	0.9591
	Meal size (g/meal)	2	93	93	0.9978
	Feeding rate (g/min)	2	46	47	0.6081
	Nº of wins (#/d)	2	9.50	8.53	
	Nº of losses (#/d)	2	9.46	8.53	

* Based on the piglet's genotype.

Grouping before on-test was successful. The IGE_{ADG} was significantly different between both groups ($P < 0.0001$) whereas the DGE_{ADG} was not different ($P = 0.60$). Before on-test, no differences were observed between high and low groups for BWT, WWT, and ON-TEST-WT. Halfway through the grower-finisher period, small differences started already to arise between both groups since the weight was significantly different in favor of the low EBV-group. The difference was somewhat larger at slaughter, although the HCW did not differ significantly.

These differences translate into a higher ADG for the low EBV-group. The difference was 24 g/d (*P*=0.0044) The high EBV-group was somewhat leaner and feed intake was lower. Feed efficiency (i.e., FCR and RES-FI) did not differ at all, nor did feed intake behavior.

After including the own performance in the GEBV's, differences in DGE_{ADG} became significant between both groups. Differences in IGE_{ADG} became smaller but remained very significant.

A pen consisted of high or low IGE_{ADG} animals only and each win in a pen implies also a loss in that pen. Therefore, the ratio is by definition equal for both groups. But the number of interactions (i.e., chasing away at the feeder) was higher in the high GEBV-group compared to the low GEBV-group, which was unexpected. This might be a sign of increased activity, which fits the higher leanness of the high EBV-group.

Differences in ADG were observed but in the unexpected direction. Van Erp – van der Kooij (2003) defined two different personalities of pigs based on their coping style during a back test: an active- and a reactive style. Animals with an active coping style showed a higher daily gain, but only in mixed groups of active and reactive animals. If group composition also matters for IGE_{ADG}, the perspective for selective breeding might be less compared to what could be expected based on the genetic variances.

3.4.2 Conclusions

At this stage of the trial, the differences in grower-finisher performance between animals with a high or low GEBV for IGE_{ADG} were small and the low EBV-group seemed to grow somewhat faster, which was unexpected. No differences were observed in feed efficiency and in (feeding) behavior. However, these are only preliminary results from the first part of the dataset, and the final analysis based on 3,000 data records should allow making clearer conclusions.

3.5 Ethic declaration

The project required blood- and fecal sampling on live animals. Sampling was done in accordance with the Dutch legislation ('Wet op Dierproeven'), which is based on EU directive 2010/63/EU on the protection of animals used for scientific purposes. In the framework of this legislation, three committees assessed the project and the accompanying sampling from different viewpoints among which social and scientific relevance, (practical) feasibility, and ethical implications. These three committees were the Central Authority for Scientific Procedures on Animals (CCD), Animal Experiment Committee (DEC) and the Animal Welfare Body of Topigs Norsvin (IvD).

As the Dutch government strives for open and transparent communication with regard to animals used for scientific purposes, the government published a laymen's summary (in Dutch) on their website: https://www.centralecommissiedierproeven.nl/onderwerpen/niet-technische-samenvatting/translationeel-of-toegepast-onderzoek/nts-2017821-varken-voer-genetica-groepshuisvesting-kopie

4. Conclusions

Including genotypes of crossbred animals in a genetic evaluation (i.e., through crossbred genomics) showed increased accuracy of the (G)EBV's. Whether the added value comes from treating purebred and crossbred traits as being different traits (for feed efficiency traits, genetic correlation between pure- and crossbreds is most likely less than 0.8 (Wientjes and Calus,

2017)), or being different traits because of Genotype x Environment interaction, or from increased number of genotyped animals was not resolved in the project.

Heritable indirect genetic effects exist and can be validated. However, the mechanisms behind this phenomenon are still poorly understood. Results presented in this report are still inconclusive despite increased numbers and power thanks to use of genomic prediction. However final analysis of data, together with analyses of ranks in these pens, should provide for a more definitive proof.

Combining knowledge on crossbred genomics while estimating breeding values for IGE_{ADG} and based on these EBV's created two divergent selected groups of animals (High/Low). If any, this setup should improve our knowledge on the mechanisms behind indirect genetic effects. In addition, the identification of feeding behavior related criteria (rank index) that showed potential to capture social interactions will complement our understanding of the responses of the high/low groups.

5. Literature

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