Estimation of heritability of feeding behaviour traits and their correlation with production traits in Finnish Yorkshire pigs

A.T. Kavlak[1] and P. Uimari[1]

[1]Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland

Correspondence

A.T. Kavlak, Department of Agricultural Sciences,
University of Helsinki, Helsinki, Finland.
Email: alper.kavlak@helsinki.fi
Tel: +358400269532

Funding Information

Raisio Oyj Tutkimussäätiö and Suomen Sianjalostuksen Säätiö

Summary

A major proportion of the costs of pork production is related to feed. The feed conversion rate (FCR) or residual feed intake (RFI) is thus commonly included in breeding programs. Feeding behaviour traits do not directly have economic value but, if correlated with production traits, can be used as auxiliary traits. The aim of this study was to estimate the heritability of feeding behaviour traits and their genetic correlations with production traits in the Finnish Yorkshire pig population. The data were available from 3235 pigs. Feeding behaviour was measured as the number of visits per day (NVD), time spent in feeding per day (TPD), daily feed intake (DFI), time spent feeding per visit (TPV), feed intake per visit (FPV) and feed intake rate (FR). The test station phase was divided into five periods. Estimates of heritabilities of feeding behaviour traits varied from 0.17 to 0.47. Strong genetic correlations were obtained between behaviour traits in all periods. However, only DFI was strongly correlated with the production traits. Interestingly, a moderate positive genetic correlation was obtained between FR and backfat thickness (0.1 – 0.5) and between FR and average daily gain (0.3 – 0.4), depending on the period. Based on the results, there is no additional benefit from including feeding-related traits other than those commonly used (FCR and RFI) in the breeding programme. However, if correlated with animal welfare the feeding behaviour traits could be valuable in the breeding programme.

Key words: eating rate, feeding behaviour, feeding rate, genetic correlation, heritability, pigs

INTRODUCTION

The profitability of pork production is dependent mainly on the production of lean meat by the efficient use of feed for growth. Thus, the most important production traits considered in pig breeding programmes are growth (average daily gain, ADG), feed conversion rate (FCR), and residual feed intake (RFI), the difference obtained between feed intake and predicted feed intake based on growth and maintenance (Kennedy et al., 1993). The genetic improvement of production traits in pigs is commonly based on the performance of group-housed pigs in a controlled test station environment. During the test period, feed intake can be measured automatically. Feeding behaviour can be measured early in life, and if it is correlated with production traits, it can be used as an early selection criterion, while pigs with unfavourable feeding behaviour can be removed from the test and replaced by other test pigs.

Estimates of the heritabilities of feeding behaviour traits range from low to high (e.g. Von Felde et al., 1996; Gilbert et al., 2007; Do et al., 2013; Lu et al., 2017). A positive genetic correlation was found between feeding behaviour and feed efficiency traits, in which animals that consume more feed per visit tend to grow faster (Labroue et al., 1997). Thus, genetic improvement in feed efficiency may also be dependent on the genetics of feeding behaviour traits, and therefore including these traits in breeding programmes has been suggested (Labroue et al., 1997; Hall et al., 1999).

The objective of this study was to estimate the heritability of feeding behaviour traits and their genetic correlations with production traits in the Finnish Yorkshire pig population. In this study, we show that feeding behaviour traits are moderately heritable and highly correlated. We also show that feeding behaviour traits, except daily feed intake, do not have a strong genetic correlation with production traits.

MATERIALS AND METHODS

Data

The data were recorded at the central test station of Figen Oy (Pietarsaari, Finland) and were available from the beginning of 2011 until 2016 (October). The pigs arrived at the test station at an average age of 89 ± 10 d (mean ± standard deviation) and an average weight of 32.7 ± 5.4 kg. During the test period (on average 95 ± 3 d), pigs were fed ad-libitum, and the feedings were recorded automatically. The feeding system was Schauer Spotmix with Schauer MLP electronic feeders and MLP-manager data management software (Schauer Agrotronic GmbH, Austria). The pigs were slaughtered (except those boars that we selected for artificial insemination) at an average age of 186 ± 10 d and an average weight of 117.7 ± 12.1 kg. The pigs were either purebred Finnish Landraces or Yorkshires or their F1-crosses. In this study, only purebred Yorkshire animals were used.

The raw data (28,964,641 observations) included transponder-id, date, time of entering the feeder, time leaving the feeder, and feed intake per visit. From the raw records time spent per visit and feeding rate per visit (g/min) were calculated. All observations that did not fulfill the following thresholds were removed from the data (see Casey et al., 2005): the feed intake per visit should be over –20 g and below 2 kg or below 20 g if the time spent per visit was 0; the time spent per visit should be more than 0 s and less than 1 h; if the feed intake per visit was less than 50 g the feeding rate per visit should be less than 500 g/min; if the feed intake per visit was more than 50 g the feeding rate per visit should be less than 170 g/min; if the feed intake was 0 g the time spent per visit should be less than 500 s; the feeding rate per visit should be more than 2 g/min; the time of entering and the time of the leaving the same feeder should not be overlapping. With these criteria, 0.5% of the raw observations were discarded, mainly because the feeding rate per visit was more than 170 g/min (given that the feed intake was over 50 g) or because the feeding rate per visit was less than 2 g/min.

From the remaining 28,826,029 observations daily values were calculated as the number of visits per day (NVD, counts), time spent in feeding per day (TPD, min), daily feed intake (DFI, g), time spent feeding per visit (TPV, min), feed intake per visit (FPV, g) and feed intake rate (FR, g/min). The TPV, FPV and FR were average values of the daily records. The final records were calculated as averages of the daily records separately for the five test periods: 0-20 days in the test, 21-40, 41-60, 61-80, and 81-93 days.

The production traits analysed were ADG, FCR, RFI, and backfat thickness (BF). FCR was defined as the feed consumption during the test period measured in feed units (1 feed unit is 9.3 MJ net energy) divided by the total growth during the test period (finishing body weight – initial body weight). The BF was an average of two Hennessy Grading Systems (type GP4, Auckland, New Zealand) measurements, one at 8 cm off the midline of the carcass behind the last rib and one at 6 cm off the midline between the third and fourth ribs. The RFI was computed as the difference between the observed and predicted DFIs, i.e. the RFI was a residual term from the linear model:

$$ADFI_{ijk} = sex_i + hys_j + b_1(IBW)_{ijk} + b_2(ADG)_{ijk} + b_3(BF)_{ijk} + e_{ijk}$$

where $ADFI_{ijk}$ is the average daily feed intake over five periods, sex_i is the sex effect (boar, gilt, castrate), hys_j is the herd*year*season interaction (four seasons were defined: January-March, April-June, July-September, October-December), b_1, b_2, and b_3 are partial regression coefficients of the initial weight at the beginning of the test period (IBW), ADG and BF, respectively.

The final data included records of 3235 Yorkshire pigs (2335 boars, 484 gilts and 416 castrates). All animals had observations for all the studied traits.

Statistical analysis

The traits were analysed, using the following animal model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_l l} + \mathbf{Z_{bp} bp} + \mathbf{e},$$

where **y** is a vector of observation (feeding behaviour traits, ADG, BF, FCR, and RFI), **b** a vector of fixed effects (sex$_i$ and hys$_j$), **X** a incidence matrix relating records to fixed effects, **a** a vector of random additive genetic effects, **l** a vector of random litter effects, **bp** a vector of random batch*pen effects and **e** a vector of random residuals; the corresponding incidence matrices are $\mathbf{Z_a}$, $\mathbf{Z_l}$ and $\mathbf{Z_{bp}}$, respectively. Pigs were from 684 different batch*pen and 174 herd*year*season combinations. The number of observations in these batch*pens varied from 1 to 12, and from 5 to 62 in herd*year*seasons. Since RFI was already corrected for sex$_i$ and hys$_j$ effects, these were not included in the linear model of RFI.

A univariate model was used for the estimation of heritability and a bi-variate model for genetic correlations. For the bi-variate model, the (co)variance matrix of the normally distributed additive genetic effects was $\mathbf{A}\otimes\mathbf{G}$, where **A** is the numerator relationship matrix, **G** the genetic (co)variance matrices of the traits and $\otimes$ denotes the Kronecker product. The (co)variance matrix of the normally distributed litter, batch*pen and residual effects were $\mathbf{I}\otimes\mathbf{B}$, $\mathbf{I}\otimes\mathbf{C}$ and $\mathbf{I}\otimes\mathbf{R}$, respectively, where **I** is an identity matrix and **B**, **C** and **R** the (co)variance matrices for litter, batch*pen and residual effects, respectively. The variance and covariance components were estimated by the restricted maximum likelihood (REML) method (Patterson & Thompson, 1971) using the DMU software (Madsen & Jansen, 2013). The pedigree data (5396 animals) included all animals with observations and their ancestors down to four generations. The average number of offspring with observations per each sire was 16.

RESULTS

Phenotypic description of the traits

The distributions of most of the traits were right-skewed (Figure 1). Prior to statistical analysis, extreme outliers (4 SD of the mean) were removed from the data. However, the data also included short visits at the feeder; thus the minimum TPV was only 32 s and the minimum FPV 13 g. Generally, older pigs visited more often at the feed station than younger animals. In contrast, the TPV decreased radically from 2.5 min (TPV1) to 1.6 min (TPV5). The total TPD increased up to 66 min/d (TPD2) and then decreased to 53 min/d (TPD5). The FPV increased from 57 g per visit (FPV1) to 89 g per visit (FPV5) and DFI from 1443 g (DFI1) to 2990 g (DFI5) from period 1 to period 5 (Figure 1). The ADG varied in this data from 588 g/d to 1268 g/d, with mean ADG of 925 ± 108 g/d. The average BF was 9.9 ± 2.1 mm, average FCR 2.5 ± 0.2, and RFI 0 ± 135 g.

Estimated heritabilities

The heritability and corresponding variance components for feeding behaviour traits are given in Table 1. The highest heritability estimate was obtained for TPV2 (0.47 ± 0.07) and the lowest for DFI1 (0.17 ± 0.05). In general, there was more variation in heritability between traits in period 1 than in later periods. In period 5, all the estimates were near 0.3; thus the heritability of the feeding behaviour traits were moderate. Overall, the lowest heritabilities were obtained for FR (from 0.19 to 0.29) than for other feeding behaviour traits. The heritability estimates of ADG, FCR and RFI were moderate (0.25 ± 0.06, 0.28 ± 0.06 and 0.32 ± 0.06, respectively) and high for BF (0.57 ± 0.07) (Table 1).

Correlations between the traits

As expected, the genetic correlations between the same behaviour trait over the various periods (1 to 5) were generally high (Figure 2). The strongest genetic correlations were obtained between adjacent periods varying from 0.96 ± 0.01 to 0.99 ± 0.01 for all behaviour traits and the weakest between periods 1 and 5, varying from 0.71 ± 0.09 (FR1 vs. FR5) to 0.83 ± 0.06 (NVD1 vs. NVD5). The phenotypic correlations within the traits were also very high throughout the periods. The strongest phenotypic correlation was obtained for FR (0.88) between periods 4 and 5, while the weakest (0.25) was obtained for DFI between periods 1 and 5.

The phenotypic and genetic correlations between the feeding behaviour traits within the same period are given in Table 2. The genetic correlations between NVD and both TPV and FPV were very high, varying from –0.79 ± 0.05 to –0.97 ± 0.01. The phenotypic correlations between these traits were also strong, varying from –0.76 to –0.83. In contrast, NVD did not correlate with the other traits. Thus, the frequency of feeding did not affect the DFI or FR. FR and TPD had a strong negative correlation; animals that show high FR have shorter TPD than animals with slow FR. The FR also had a moderately positive genetic correlation between the DFI varying from 0.22 ± 0.14 (period 4) to 0.4 ± 0.12 (period 5). Thus, animals with genetic background of high FR also tend to have a genetic background of higher DFI.

Most of the correlations between feeding behaviour traits and production (ADG, BF, FCR and RFI) traits did not differ from zero (Table 3). Only DFI had strong positive genetic correlations with all the production traits (Table 3 and Figure 3); a favourable correlation with ADG, but unfavourable correlations with BF, FCR, and RFI. In addition, the FPV had a moderately positive (unfavourable) correlation with BF; animals that consume large quantities of feed per visit tend to gain more BF. The genetic correlation between FPV and BF increased from periods 1 to 5. BF was also correlated with FR; animals with high FR tend to gain more BF as well. This correlation became smaller from periods 1 to 5. In addition, the genetic correlation between TPD and RFI varied from 0.34 ± 0.13 (period 2) to 0.45 ± 0.13 (period 5), thus animals with more TPD also show increased RFI.

All correlations between the production traits were significant. The genetic correlation between FCR and BF was 0.79 ± 0.07, but only 0.37 ± 0.16 between FCR and ADG (Table 3). In contrast, the genetic correlations between RFI and BF was only 0.38 ± 0.12 while between RFI and ADG 0.63 ± 0.13. Thus, selection for RFI more strongly affects ADG than BF, while selection for FCR more strongly affects BF than ADG.

DISCUSSION

Feeding behaviour and production traits

In this study, the performance of pigs at the test station was divided into five 20-d periods, starting 3 d after arrival at the test station. In the previous study of Von Felde et al. (1996), the feed intake was measured during five periods (every second week) over 10 weeks. Rauw et al. (2006) and Schulze et al. (2003) also used five periods, while Young et al. (2009) measured feeding behaviour traits over three periods: the entire test (from approximately 3 to 8 months of age), the first half of the test, and the second half of the test. Chen et al. (2010b) also used three periods (85 - 106, 107 - 128 and 129 - 150 days of age). The data can also be analysed, using a random regression model as applied to body weight and feed intake by Wetten et al. (2012) and Coyne et al. (2017). However, based on our results and those of other authors, division of the test period into five parts enabled us to demonstrate possible differences in heritabilities and genetic covariances between various growth phases of fattening pigs.

The mean TPD (61 min), DFI (2.2 kg) and FR (40 g/min) over five periods were similar to those reported by Do et al. (2013) (62 min, 2.1 kg, and 37 g/min) in Yorkshire and slightly larger than those reported by Labroue et al. (1999) also in Yorkshire (50 min, 1.7 kg and 35 g/min). In addition, the tendency for feeding behaviour traits to vary over time in our study was similar to that reported by other authors. Reyer et al. (2017) reported that Maxgro line (Hermitage Genetics, Ireland) pigs tended to visit the feeder more often, but spent less time there as they aged, while older pigs showed higher FRs than younger pigs.

The average production performances (ADG, BF and FCR) of the test pigs in this study from 2011 to 2016 were 925 g, 9.9 mm and 2.5, respectively. Similar test station performances have also been reported in other recent studies in different breeds, e.g. Jiao et al. (2014), Do et al. (2013), Bahelka et al. (2015), and Godinho et al. (2018). Thus, Finnish Yorkshires have similar growth performance than other recently studied pig breeds. The RFI was calculated as the difference between the observed and predicted DFI based on IBW, ADG and BF (also corrected for sex and herd*year*season effects). The RFI varied from –505 g to 878 g, with SD of 135 g. Similar RFI SDs were also obtained by Cai et al. (2008) and Dekkers and Gilbert (2010) in Yorkshire.

Estimates of heritability

The heritability of the feeding behaviour traits varied over time (from period 1 to 5), but the genetic correlations between the same trait over time were high for all traits (Figure 2). Thus, the genetic basis for feeding behaviour at the beginning of the test was similar to that at the end. The estimated heritabilities were slightly lower in the first period than in later periods, especially for DFI. The young pigs at the beginning of the test may have been more vulnerable to environmental factors than older pigs. Our statistical model with sex, herd*year*season, litter and batch*pen effects may not have been sensitive enough to record all the environmental factors influencing the feeding behaviour of young pigs. Factors such as adaptation to new pen mates and feeding systems may have influenced the estimates.

In addition, the estimated heritabilities between traits varied more at the beginning of the test (period 1) than at the end (period 5). The heritabilities of all the feeding behaviour traits in period 5 converged to an approximate value of 0.3. Similar heritabilities have been obtained in other studies. For example, Hall et al. (1999) obtained heritabilities varying from 0.27 (FPV) to 0.34 (NVD) in Yorkshire, Schulze et al. (2003) from 0.34 (NVD) to 0.46 (TPD) in a combined data of Yorkshire and Landrace based dam lines, and Chen et al. (2010a) from 0.18 (TPD) to 0.42 (FR) in Duroc. Our estimates for DFI were higher than those obtained by Coyne et al. (2017) (0.07 to 0.25), in which a random regression model and combined Finnish Landrace and Yorkshire data were used. This could have been due to the difference in statistical approaches (logistic regression vs. periodic approach) and data (all breed data vs. single breed data). However, our estimates for DFI were similar to those presented by Hall et al. (1999), in which the heritabilities ranged from 0.18 to 0.26 over the four test periods. The estimates of the heritability of production traits (ADG, BF and FCR) were moderate and similar to those obtained in other studies (see Clutter, 2011).

Genetic correlations

Strong negative genetic correlations were obtained between NVD and FPV (over –0.9 in all periods) and between NVD and TPV (–0.79 to –0.88). Also, a strong positive correlation was obtained between FPV and TPV (0.83 to 0.90). As discussed above, these strong correlations were reasonable. To obtain sufficient energy and nutrients for maintenance and growth, the pigs either consume feed often but in small portions or more seldom and in large portions. In addition, FR had a moderately genetic correlation between DFI (0.22 to 0.40) in all periods; thus faster eaters (g/min) tended to have higher genetic potential for DFI. A strong genetic correlation was also obtained with FR and TPD especially early in the test period. Do et al. (2013) also reported highly negative genetic correlations between NVD and FPV (–0.95) and between NVD and TPV (–0.91) in Danish Yorkshire populations, as well as a significant positive correlation between DFI and FR (0.36). Schulze et al. (2003) also reported highly negative genetic correlations between NVD and FPV (–0.92) and between NVD and TPV (–0.81), a highly positive correlation between FPV and TPV (0.86) and a moderately positive correlation between DFI and FR (0.20) in a combined data of Yorkshire and Landrace based dam lines.

Among the feeding traits examined, the DFI showed the highest genetic correlation between all production traits. These correlations were exceptionally high in the first period (0.65 to 0.89) and slightly lower in the last period (0.60 to 0.86). The genetic correlation between DFI and ADG increased from period 1 (0.67) to period 5 (0.86), while the remaining genetic correlations (between DFI and BF, FCR and RFI) decreased over time. A positive genetic correlation between DFI and ADG was also reported by Jiao et al. (2014) (0.32), Chen et al. (2010a) (0.46), Do et al. (2013) (0.84), Cai et al. (2008) (0.88) and between DFI and BF by Jiao et al. (2014) (0.36), Do et al. (2013) (0.68), and Cai et al. (2008) (0.57). Given that a high genetic correlation was obtained only between DFI and production traits, there is no reason to include feeding behaviour traits in the breeding programme. However, if there exist correlation between feeding behaviour traits and animal welfare related traits such as tail biting, as indicated by Wallenbeck and Keeling (2013), then using feeding behaviour traits as auxiliary traits to improve animal welfare should be considered in breeding programs.

One of the most interesting genetic correlations was that between FR1 and BF (0.51). Thus, animals with the genetic potential for fast FR early in the test (period 1) also gain more fat. Later in the test, the genetic correlation between FR and BF decreased to 0.15 (period 5). In contrast to FR, the genetic correlation between FPV and BF strengthened from periods 1 (0.32) to 5 (0.46). A positive genetic correlation between FR and BF was found by Schulze et al. (2003) (0.16) and Do et al. (2013) (0.26), but none between FPV and BF (Schulze et al., 2003) (0.09), while a weaker correlation (0.25) was found by Do et al. (2013).

Interestingly in humans, a positive association was obtained between eating speed and overweight (Tanihara et al., 2011; Lee et al., 2016) and eating speed and metabolic syndrome among other health problems (Tajima et al., 2014; Nohara et al., 2015; Zhu et al., 2015; Tao et al., 2018). Fast eaters tend to be more obese, have higher blood pressure and be more susceptible to metabolic diseases than slow eaters. The estimated odds ratio between normal and fast eating individuals for overweight in the Japanese adult population was 1.9 (Lee et al., 2016) and between slow and fast eating individuals for metabolic syndrome in the Chinese adult population 2.3 (Tao et al., 2018). Given the similar metabolic system in pigs and humans, pigs can be used as an animal model for further investigation of the mechanism behind the unfavourable association between eating (or feeding) speed and accumulation of body fat.

CONCLUSIONS

In this study, the heritability of feeding behaviour traits and their correlation with production traits were investigated in the Finnish Yorkshire pig population. The results indicated moderate heritability for all studied feeding behaviour traits. High genetic correlations were obtained only between DFI and production traits. The most interesting correlation was obtained between FR (and FPV) and BF. High breeding values for FR (g/min) early in the test or large portion sizes late in the test indicate a genetic potential to gain BF. However, the potential utilization of this correlation is limited in pig breeding programmes even though selection against FR does not seem to affect other production traits. BF is highly heritable; thus direct selection of BF based on information from relatives or ultrasound measurement of the animal itself is more effective than indirect selection based on early FR. In the selection of sow replacement at the farm level, favouring piglets that consume feed rapidly may in turn favour sows that have greater fat reservoirs for farrowing and feeding the litter. Finally, since a positive correlation between eating speed and overweight has been demonstrated in human populations, studies in pigs may aid in revealing the genetic basis of this unfavourable association.

ACKNOWLEDGEMENTS

The authors thank Raisio Oyj Tutkimussäätiö and Suomen Sianjalostuksen Säätiö for funding this research. We are grateful to Figen Oy for providing the data and M.Sc. Anna Riihimäki for help in editing the data.

REFERENCES

Bahelka, I., Tomka, J., Bucko, O., & Hanusova, E. (2015). Growth performance and carcass quality of entire males, surgical castrates and gilts. *Slovak Journal of Animal Science, 48,* 116–121.

Cai, W., Casey, D. S., & Dekkers, J. C. M. (2008). Selection response and genetic parameters for residual feed intake in Yorkshire swine. *Journal of Animal Science, 86,* 287–298.

Casey, D. S., Stern, H. S., & Dekkers, J. C. M. (2005). Identification of errors and factors associated with errors in data from electronic swine feeders. *Journal of Animal Science, 83,* 969–982.

Chen, C. Y., Misztal, I., Tsuruta, S., Herring, W.O., Holl, J., & Culbertson, M. (2010a). Influence of heritable social status on daily gain and feeding pattern in pigs. *Journal of Animal Breeding and Genetics, 127,* 107-112.

Chen, C. Y., Misztal, I., Tsuruta, Zumbach, B., S., Herring, W.O., Holl, J., & Culbertson, M. (2010b). Estimation of genetic parameters of feed intake and daily gain in Durocs using data from electronic swine feeders. *Journal of Animal Breeding and Genetics, 127,* 230-234.

Clutter, A. C. (2011). Genetics of performance traits. In The genetics of the pig. 2nd Edn. (editors M.F. Rotschild and A. Ruvinsky). CAB International 2011.

Coyne, J. M., Donagh, P. B., Matilainen, K., Sevon-Aimonen, M.-L., Mäntysaari, E. A., Juga, J. K., Serenius, T., & McHugh, N. (2017). Genetic co-variance functions for live weight, feed intake, and efficiency measures in growing pigs. *Journal of Animal Science, 95,* 0021-8812.

Dekkers, J. C. M. & Gilbert, H. (2010). Genetic and Biological Aspect of Residual Feed Intake in Pigs. Proceedings of the 9th world congress on genetics applied to livestock production: 1–6 August 2010; Leipzig.

Do, D. N., Strathe, A. B., Jensen, J., Mark T., & Kadarmideen, H. N. (2013). Genetic parameters for different measures of feed efficiency and related traits in boars of three pig breeds. *Journal of Animal Science, 91,* 4069-4079.

Gilbert, H., Bidanel, J. P., Gruand, J., Cartitez, J. C., Billon, Y., Guillouet, P., Lagant, H., Noblet, J., & Sellier, P. (2007). Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. *Journal of Animal Science, 85,* 3182-3188.

Godinho, R. M., Bastiaansen, J. W. M., Sevillano, C. A., Silva, F. F., Guimarães, S. E. F., & Bergsma, R. (2018). Genotype by feed interaction for feed efficiency and growth performance traits in pigs. *Journal of Animal Science, 96,* 4125–4135.

Hall, A., Hill, W., Bampton, P., & Webb, A. (1999). Genetic and phenotypic parameter estimates for feeding pattern and performance test traits in pigs. *Animal Science, 68,* 43-48.

Jiao, S., Maltecca, C., Gray, K. A., & Cassady, J. P. (2014). Feed intake, average daily gain, feed efficiency, and real-time ultrasound traits in Duroc pigs: I. Genetic parameter estimation and accuracy of genomic prediction. *Journal of Animal Science, 92,* 2377–2386.

Kennedy, B. W., Van der Werf, J. H., & Meuwissen, T. H. (1993). Genetic and statistical properties of residual feed intake. *Journal of Animal Science, 71,* 3239–3250.

Labroue, F., Gueblez, R., & Sellier, P. (1997). Genetic parameters of feeding behaviour and performance traits in group-housed Large White and French Landrace growing pigs. *Genetic Selection Evolution, 29,* 451–468.

Labroue, F., Gueblez, R., Meunier-Salaun, M. C., & Sellier, P. (1999). Feed intake behaviour of group-housed Pietrain and Large White growing pigs. *Annales de zootechnie, INRA/EDP Sciences, 48,* 247 -261.

Lee, J. S., Mishra, G., Hayashi, K., Watanabe, E., Mori, K., & Kawakubo, K. (2016). Combined eating behaviors and overweight: eating quickly, late evening meals, and skipping breakfast. *Eating Behaviors, 21,* 84–88.

Lu, D., Jiao, S., Tiezzi, F., Knauer, M., Huang, Y., Gray, K. A., & Maltecca, C. (2017). The relationship between different measures of feed efficiency and feeding behavior traits in Duroc pigs. *Journal of Animal Science, 95,* 3370–3380.

Madsen, P., & Jensen, J. (2013). *A user's guide to DMU. A package for analyzing multivariate mixed models.* Version 6, release 5.2. University of Aarhus, Center for Quantitative Genetics and Genomics, Department of Molecular Biology and Genetics, Research Centre Foulum, Tjele, Denmark.

Nohara, A., Maejima, Y., Shimomura, K., Kumamoto, K., Takahashi, M., & Akuzawa, M. (2015). Self-awareness of fast eating and its impact on diagnostic components of metabolic syndrome among middle-aged Japanese males and females. *Endocr Regul, 49,* 91–96.

Patterson, HD. & Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal. *Biometrika, 58,* 545-554.

Rauw, W. M., Soler, J., Tibau, J., Reixach, J., & Gomez Raya, L. (2006). Feeding time and feeding rate and its relationship with feed intake, feed efficiency, growth rate, and rate of fat deposition in growing Duroc barrows. *Journal of Animal Science, 84,* 3404–3409.

Reyer, H., Shirali, M., Ponsuksili, S., Murani, E., Varley, P. F., Jensen, J., & Wimmers, K. (2017). Exploring the genetics of feed efficiency and feeding behaviour traits in a pig line highly selected for performance characteristics. *Molecular Genetics and Genomics, 292,* 1001-1011.

Schulze, V., Roehe R., Bermejo, J. L., Looft, H., & Kalm, E. (2003). The influence of feeding behaviour on feed intake curve parameters and performance traits of station-tested boars. *Livestock Production Science, 82,* 105–116.

Tajima, M., Lee, J. S., Watanabe, E., Park, J. S., Tsuchiya, R., & Fukahori, A. (2014). Association between changes in 12 lifestyle behaviors and the development of metabolic syndrome during 1 year among workers in the Tokyo metropolitan area. *Circulation Journal, 78,* 1152–1159.

Tanihara, S., Imatoh, T., Miyazaki, M., Babazono, A., Momose, Y., & Baba, M. (2011). Retrospective longitudinal study on the relationship between 8-year weight change and current eating speed. *Appetite, 57,* 179–183.

Tao, L., Yang, K., Huang, F., Liu, X., Li, X., Luo, Y., Wu, L., & Guo, X. (2018). Association between self-reported eating speed and metabolic syndrome in a Beijing adult population: a cross-sectional study. *BMC Public Health, 18,* 855.

Von Felde, A., Roehe, R., Looft, H., & Kalm, E. (1996). Genetic association between feed intake and feed intake behaviour at different stages of growth of group-housed boars. *Livestock Production Science, 47,* 11-12.

Wallenbeck, A., & Keeling, L. J. (2013). Using data from electronic feeders on visit frequency and feed consumption to indicate tail biting outbreaks in commercial pig production. *Journal of Animal Science, 91,* 2879-2884.

Wetten, M., Ødegård, J., Vangen, O., & Meuwissen, T. (2012). Simultaneous estimation of daily weight and feed intake curves for growing pigs by random regression. *Animal, 6,* 433-439.

Young, J., Cai, W., Nettleton, D. S., & Dekkers, J. C. M. (2009). Feeding Behavior of Yorkshire Pigs Selected for Residual Feed Intake. *Animal Industry Report: AS 655,* R2454.

Zhu, B., Haruyama, Y., Muto, T., & Yamazaki, T. (2015). Association between eating speed and metabolic syndrome in a three-year population-based cohort study. *Journal of Epidemiology, 25,* 332–336.

TABLE 1 Heritability (h^2) and variances of additive genetic (σ^2_a), litter (σ^2_l), batch*pen (σ^2_{bp}), and residual (σ^2_e) effects of feeding behaviour and production traits.

Trait	**h^2**	**SE(h^2)**	**σ^2_a**	**σ^2_l**	**σ^2_{bp}**	**σ^2_e**
Period 1						
NVD1	0.36	0.06	44.4	12.3	20.0	41.8
TPD1	0.37	0.06	51.1	17.1	2.9	62.7
DFI1	0.17	0.05	9572	9814	10691	22881
TPV1	0.38	0.07	0.28	0.07	0.11	0.26
FPV1	0.44	0.07	198.3	44.7	56.6	142.7
FR1	0.19	0.06	5.6	2.8	9.9	11.0
Period 2						
NVD2	0.41	0.06	72.1	14.9	23.4	62.0
TPD2	0.36	0.06	58.3	17.1	9.6	76.4
DFI2	0.26	0.06	22405	11264	14411	36879
TPV2	0.47	0.07	0.41	0.04	0.12	0.28
FPV2	0.43	0.07	324.3	56.9	114.7	244.0
FR2	0.21	0.06	9.4	3.0	9.5	21.6
Period 3						
NVD3	0.37	0.06	95.6	17.6	41.7	99.6
TPD3	0.34	0.06	51.5	13.9	10.3	74.4
DFI3	0.30	0.06	36238	10854	17839	53845
TPV3	0.36	0.06	0.28	0.04	0.13	0.32
FPV3	0.34	0.06	368.3	95.3	186.0	423.1
FR3	0.26	0.06	22.9	5.4	12.6	39.9
Period 4						
NVD4	0.37	0.06	105.0	13.1	44.6	116.7
TPD4	0.36	0.06	47.9	8.4	7.7	64.9
DFI4	0.32	0.06	54448	14064	22324	74246
TPV4	0.37	0.06	0.23	0.03	0.09	0.26
FPV4	0.36	0.06	482.9	97.9	201.1	528.9
FR4	0.28	0.06	39.3	8.5	20.8	68.9
Period 5						
NVD5	0.31	0.06	99.4	17.7	47.9	147.0
TPD5	0.28	0.06	36.8	7.9	11.3	68.9
DFI5	0.29	0.06	71959	16457	25757	125164
TPV5	0.34	0.06	0.19	0.03	0.08	0.24
FPV5	0.32	0.06	493.7	116.8	218.6	694.9
FR5	0.29	0.06	61.1	11.1	27.5	110.6
Production traits						
ADG	0.25	0.06	2661	1576	697	5439
BF	0.57	0.07	1.93	0.22	0.12	1.06
FCR	0.28	0.06	0.010	0.002	0.007	0.017
RFI	0.32	0.06	6749	1359	3320	9104

NVD: Number of visits per day, TPD: Time spent in feeding per day, DFI: Daily feed intake, TPV: Time spent feeding per visit, FPV: Feed intake per visit, FR: Feed intake rate, ADG: Average daily gain, BF: Backfat thickness, FCR: Feed conversion rate, RFI: Residual feed intake.

TABLE 2 Phenotypic (below diagonal) and genetic correlation (above diagonal) between feeding behaviour traits within the same period. Standard errors are given in brackets.

Trait	**NVD1**	**TPD1**	**DFI1**	**TPV1**	**FPV1**	**FR1**
Period 1						
NVD1		0.50 (0.11)	0.18 (0.17)	–0.79 (0.05)	–0.91 (0.03)	–0.06 (0.15)
TPD1	0.20		0.17 (0.17)	0.09 (0.13)	–0.36 (0.12)	–0.74 (0.08)
DFI1	0.10	0.22		0.04 (0.17)	0.25 (0.16)	0.40 (0.16)
TPV1	–0.76	0.28	0.03		0.83 (0.04)	–0.31 (0.14)
FPV1	–0.77	–0.11	0.35	0.80		0.24 (0.14)
FR1	0.10	–0.52	0.51	–0.31	0.17	
Period 2						
	NVD2	TPD2	DFI2	TPV2	FPV2	FR2
NVD2		0.10 (0.13)	0.01 (0.14)	–0.83 (0.04)	–0.93 (0.02)	0.17 (0.14)
TPD2	0.05		0.27 (0.14)	0.45 (0.10)	0.08 (0.13)	–0.75 (0.07)
DFI2	0.05	0.26		0.17 (0.13)	0.36 (0.12)	0.29 (0.15)
TPV2	–0.77	0.39	0.07		0.89 (0.02)	–0.56 (0.10)
FPV2	–0.80	0.01	0.33	0.84		–0.09 (0.15)
FR2	0.20	–0.59	0.42	–0.42	0.01	
Period 3						
	NVD3	TPD3	DFI3	TPV3	FPV3	FR3
NVD3		–0.01 (0.13)	0.03 (0.14)	–0.86 (0.03)	–0.97 (0.01)	0.28 (0.13)
TPD3	0.01		0.21 (0.14)	0.50 (0.10)	0.11 (0.14)	–0.77 (0.06)
DFI3	0.05	0.24		0.11 (0.14)	0.32 (0.13)	0.29 (0.14)
TPV3	–0.78	0.40	0.05		0.87 (0.03)	–0.60 (0.10)
FPV3	–0.82	0.04	0.27	0.86		–0.16 (0.15)
FR3	0.27	–0.64	0.37	–0.49	–0.11	
Period 4						
	NVD4	TPD4	DFI4	TPV4	FPV4	FR4
NVD4		–0.07 (0.13)	0.01 (0.13)	–0.88 (0.03)	–0.94 (0.02)	0.32 (0.12)
TPD4	–0.01		0.28 (0.13)	0.51 (0.10)	0.17 (0.13)	–0.80 (0.06)
DFI4	0.11	0.29		0.15 (0.13)	0.34 (0.12)	0.22 (0.14)
TPV4	–0.80	0.40	0.03		0.89 (0.02)	–0.60 (0.09)
FPV4	–0.83	0.08	0.22	0.88		–0.20 (0.14)
FR4	0.34	–0.63	0.37	–0.53	–0.18	

Period 5						
	NVD5	TPD5	DFI5	TPV5	FPV5	FR5
NVD5		–0.03 (0.14)	0.06 (0.14)	–0.83 (0.04)	–0.90 (0.03)	0.35 (0.12)
TPD5	0.00		0.31 (0.13)	0.57 (0.10)	0.26 (0.13)	–0.66 (0.08)
DFI5	0.18	0.41		0.17 (0.14)	0.34 (0.13)	0.40 (0.12)
TPV5	–0.78	0.39	0.02		0.90 (0.02)	–0.63 (0.09)
FPV5	–0.81	0.12	0.18	0.90		–0.24 (0.14)
FR5	0.36	–0.57	0.35	–0.52	–0.21	

NVD: Number of visits per day, TPD: Time spent in feeding per day, DFI: Daily feed intake, TPV: Time spent feeding per visit, FPV: Feed intake per visit, FR: Feed intake rate.

TABLE 3 Phenotypic (r_p) and genetic correlation (r_g) between production and feeding behaviour traits. Standard errors (SE) are given in brackets.

Traits	ADG		BF		FCR		RFI	
Period 1	r_p	r_g (SE)	r_p	r_g (SE)	r_p	r_g (SE)	r_p	r_g (SE)
NVD1	–0.02	–0.01 (0.15)	–0.08	–0.05 (0.13)	–0.02	0.18 (0.14)	0.13	0.13 (0.15)
TPD1	0.09	–0.04 (0.15)	0.01	–0.05 (0.13)	0.03	0.34 (0.13)	0.15	0.42 (0.13)
DFI1	0.45	0.67 (0.12)	0.33	0.65 (0.11)	0.34	0.88 (0.08)	0.30	0.89 (0.10)
TPV1	0.07	0.00 (0.15)	0.11	0.14 (0.13)	–0.02	0.10 (0.14)	–0.04	0.15 (0.14)
FPV1	0.21	0.17 (0.15)	0.23	0.32 (0.11)	0.11	0.21 (0.13)	0.01	0.18 (0.14)
FR1	0.18	0.38 (0.15)	0.15	0.51 (0.12)	0.25	0.31 (0.16)	0.14	0.12 (0.16)
Period 2								
NVD2	–0.02	–0.03 (0.14)	–0.08	–0.07 (0.12)	0.08	0.19 (0.13)	0.14	0.17 (0.13)
TPD2	0.12	0.23 (0.15)	0.10	0.17 (0.12)	0.04	0.18 (0.14)	0.14	0.34 (0.13)
DFI2	0.60	0.88 (0.05)	0.46	0.72 (0.07)	0.35	0.76 (0.09)	0.36	0.85 (0.08)
TPV2	0.08	0.10 (0.14)	0.13	0.22 (0.12)	–0.03	–0.01 (0.14)	–0.04	–0.00 (0.14)
FPV2	0.25	0.29 (0.13)	0.27	0.43 (0.10)	0.07	0.08 (0.14)	0.01	0.04 (0.14)
FR2	0.24	0.30 (0.16)	0.15	0.25 (0.14)	0.20	0.29 (0.16)	0.16	0.19 (0.16)
Period 3								
NVD3	–0.05	–0.04 (0.15)	–0.11	–0.18 (0.12)	0.09	0.07 (0.14)	0.17	0.11 (0.14)
TPD3	0.14	0.19 (0.15)	0.12	0.09 (0.13)	0.02	0.22 (0.14)	0.13	0.40 (0.13)
DFI3	0.68	0.91 (0.04)	0.51	0.64 (0.08)	0.34	0.74 (0.09)	0.44	0.88 (0.07)
TPV3	0.10	0.12 (0.15)	0.15	0.25 (0.12)	–0.05	0.03 (0.14)	–0.07	0.04 (0.14)
FPV3	0.27	0.32 (0.14)	0.28	0.47 (0.11)	0.03	0.17 (0.14)	–0.01	0.10 (0.14)
FR3	0.24	0.29 (0.15)	0.13	0.24 (0.13)	0.19	0.12 (0.16)	0.19	0.05 (0.16)
Period 4								
NVD4	–0.04	–0.10 (0.15)	–0.10	–0.22 (0.12)	0.09	0.03 (0.14)	0.17	0.09 (0.14)
TPD4	0.14	0.23 (0.15)	0.15	0.17 (0.12)	0.01	0.30 (0.13)	0.10	0.36 (0.13)
DFI4	0.71	0.88 (0.04)	0.52	0.60 (0.08)	0.30	0.75 (0.09)	0.46	0.85 (0.07)

TPV4	0.11	0.26 (0.14)	0.14	0.29 (0.12)	–0.06	0.07 (0.14)	–0.08	0.04 (0.14)
FPV4	0.28	0.22 (0.15)	0.27	0.44 (0.11)	0.02	0.17 (0.14)	–0.01	0.11 (0.14)
FR4	0.25	0.31 (0.15)	0.12	0.11 (0.13)	0.19	0.04 (0.15)	0.24	0.05 (0.15)
Period 5								
NVD5	–0.04	–0.08 (0.15)	–0.07	–0.20 (0.13)	0.08	0.06 (0.15)	0.17	0.08 (0.14)
TPD5	0.14	0.31 (0.15)	0.16	0.22 (0.13)	0.03	0.36 (0.14)	0.17	0.45 (0.13)
DFI5	0.61	0.86 (0.05)	0.50	0.60 (0.08)	0.26	0.73 (0.10)	0.49	0.83 (0.07)
TPV5	0.11	0.33 (0.14)	0.15	0.31 (0.12)	–0.03	0.10 (0.14)	–0.05	0.11 (0.14)
FPV5	0.27	0.46 (0.13)	0.27	0.46 (0.11)	0.02	0.20 (0.14)	0.02	0.11 (0.15)
FR5	0.25	0.30 (0.14)	0.13	0.15 (0.13)	0.17	0.05 (0.15)	0.24	0.11 (0.15)
ADG			0.49	0.37 (0.12)	–0.21	0.37 (0.16)	0.02	0.63 (0.13)
BF					0.24	0.79 (0.07)	0.02	0.38 (0.12)
FCR							0.79	0.79 (0.06)

NVD: Number of visits per day, TPD: Time spent in feeding per day, DFI: Daily feed intake, TPV: Time spent feeding per visit, FPV: Feed intake per visit, FR: Feed intake rate, ADG: Average daily gain, BF: Backfat thickness, FCR: Feed conversion rate, RFI: Residual feed intake.

Figure Legends

Figure 1 Box-plots of the feeding behaviour traits over the five periods.

Figure 2 Phenotypic (below diagonal) and genetic correlations (above diagonal) between the same behaviour trait over the five periods.

Figure 3 Genetic correlations between the feeding behaviour traits and the production traits. Only statistically significant (P-value < 0.05) correlations are shown.

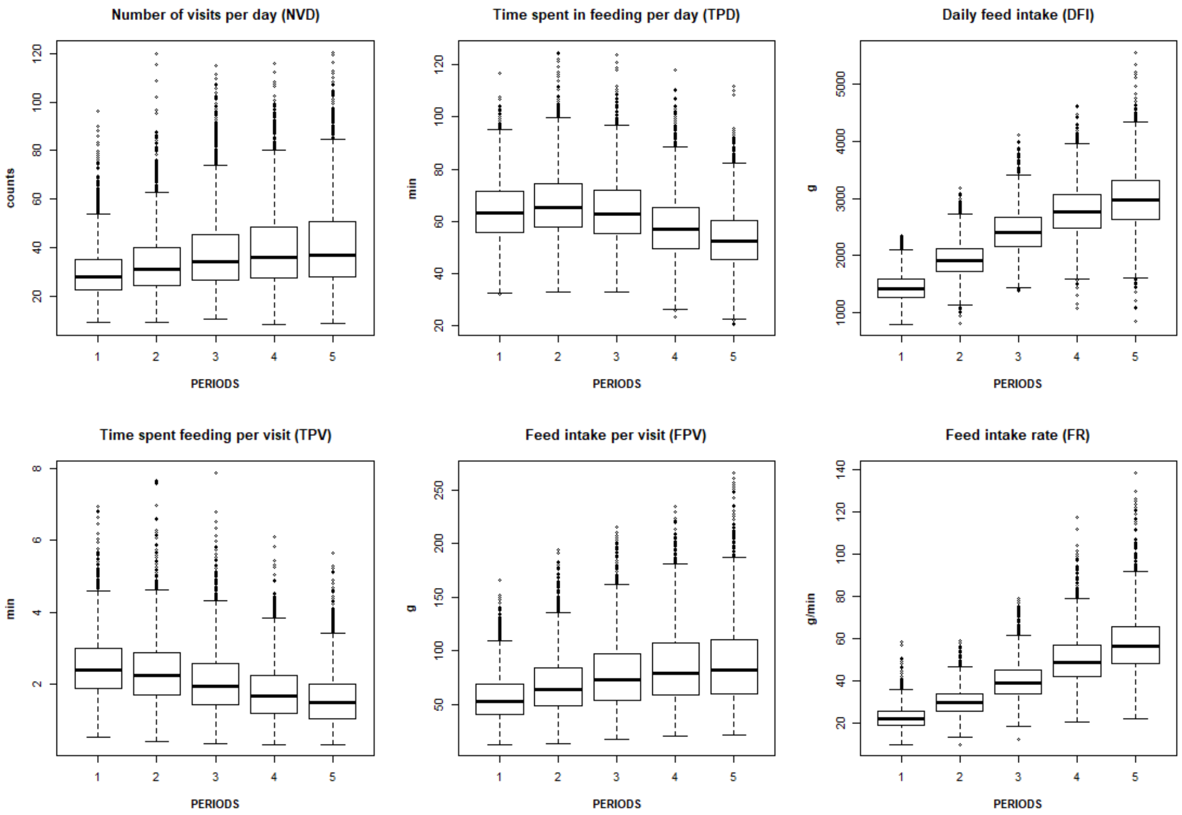

Figure 1 Box-plots of the feeding behaviour traits over the five periods.

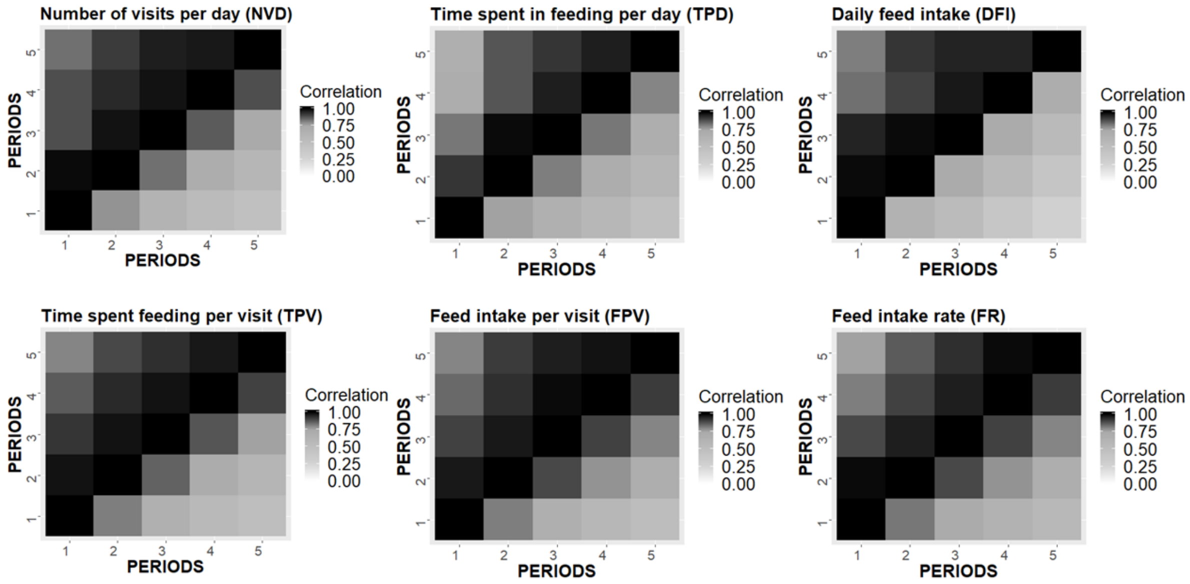

Figure 2 Phenotypic (below diagonal) and genetic correlations (above diagonal) between the same behaviour trait over the five periods.

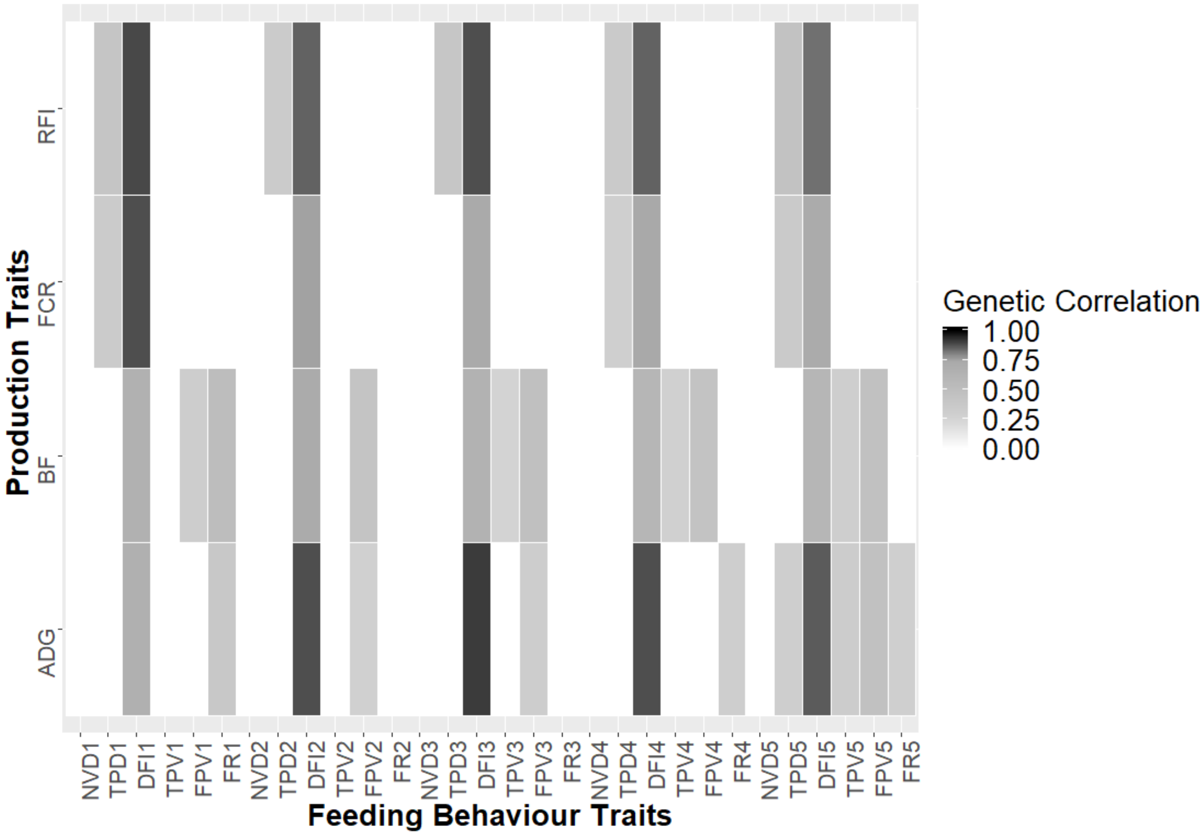

Figure 3 Genetic correlations between the feeding behaviour traits and the production traits. Only statistically significant (P-value < 0.05) correlations are shown.