Genetic analysis of protein efficiency and its association with performance and meat quality traits under a protein-restricted diet

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Abstract

Background

An essential component in the development of a sustainable pig production is the reduction of nitrogen excretion in fattening pigs. Pig feeds typically contain high levels of dietary crude protein, and due to incomplete conversion to muscle tissue, excess nitrogen is excreted, resulting in environmental problems such as nitrate pollution and greenhouse gas emissions. Therefore, improving protein efficiency (PE), i.e. the proportion of dietary protein that remains in the carcass and is thus available for meat production, is desirable. This study aimed to estimate the heritability (h^2) of PE and its genetic correlations with phosphorus efficiency, three performance, seven meat quality and two carcass quality traits when pigs were fed a 20% protein-restricted diet, using a total of 1,071 Swiss Large White pigs. To determine PE, the intake of feed with known nutrient content was accurately recorded for each pig and the nitrogen and phosphorus content of the carcass was determined using dual-energy X-ray absorptiometry. Genetic analysis was performed with a Bayesian animal model.

Results

We found an average PE of 0.39 ± 0.04 and a heritability of 0.43 (0.29, 0.58). PE showed a low genetic correlation with phosphorus efficiency (0.12 [0.04, 0.21]) and moderate genetic correlations with feed conversion ratio (-0.40 [-0.50, -0.30]), average daily gain (-0.34 [-0.41, -0.23]) and average daily feed intake (-0.61 [-0.69, -0.50]). The genetic correlations between PE and meat quality traits were not significantly different from zero except for meat redness (-0.40 [-0.58, -0.09]) and meat yellowness (-0.27 [-0.45, -0.04]). In contrast, feed conversion ratio showed unfavourable genetic correlations with meat colour, drip loss and cooking loss.

Conclusions

Protein efficiency is heritable and can be considered in breeding to reduce the environmental impact of pig production without influencing meat quality traits, but the potential for

coselecting improved phosphorus efficiency is rather small. Selecting nutrient efficiencies might be a more suitable strategy to reduce nitrogen pollution from manure than focusing on FCR because the latter shows genetic antagonism with meat quality in our population.

Background

In the past, the focus of animal breeding had been on improving production traits, but today, sustainability concerns are increasingly gaining importance. An essential component to consider in the development of a sustainable pig production chain is the reduction of nitrogen excretion in fattening pigs. Compared to other crops, soybeans contain the highest amount of lysine, which is why soybean meal is often included in the feed in order to meet the lysine requirements of pigs, resulting in high dietary crude protein content in the feed (Wang et al., 2018). Consequently, there is increased excretion of excess nitrogen in feces and urine, which contributes significantly to environmental problems such as nitrate pollution (Notarnicola et al., 2017) and greenhouse gas emissions in the form of nitrous oxide when manure is applied to pastures and fields (Del Grosso et al., 2022). Besides pollution, the large-scale export of soybean from South America has caused massive deforestation in this region, loss of terrestrial biodiversity and deterioration of ecosystem services (Foley et al., 2005). In addition, the increasing demand for meat, as a result of rapid growth of the world population, has led to massive expansion of land for soybean cultivation, thereby displacing natural vegetation and other crop cultivation (Graesser et al., 2018). Therefore, considering the environmental and social impact of pig production, it is essential to improve protein efficiency (PE) in pigs. Protein efficiency is defined as the proportion of total dietary protein intake that is retained in the carcass and thus available for meat production. An improvement in PE would simultaneously decrease protein excretion, thereby reducing the contribution of pigs to environmental pollution and greenhouse gas emission. Since more than 50% of the ingested dietary protein in pigs is excreted as waste (Millet et al., 2018; Kasper et al., 2020a), nutrition is an important factor to consider in improving PE. Pomar and Remus (2019) reported that for every percent reduction in dietary nitrogen, nitrogen excretion could be decreased by 1.5%, thus improving PE. While the final body weight in each, grower and

finisher phase, did not differ significantly between pigs on a control and a 20% protein-reduced diet, the days on feed in each phase were significantly longer for pigs receiving the protein-reduced diet. For instance, castrated males took 2.5 days longer in both the grower and finisher phase and females took 5.9 and 8.4 days longer in grower and finisher phase, respectively). However, in addition to nutritional strategies to improve PE, a genetic solution can be sought. Ruiz-Ascacibar et al. (2017), who investigated the influence of different levels of dietary protein on the PE of the Swiss Large White pig population, reported that PE varies between 37.5 and 55%. This variation between individuals to retain dietary protein can be exploited for the purpose of breeding. Additionally, since excreted phosphorus also contributes to environmental pollution, it is interesting to investigate the relationship of PE with phosphorus efficiency for a possible co-selection of this trait.

Feed conversion ratio (FCR) and residual feed intake (RFI) are the two most commonly applied traits in improving feed efficiency, and both are economically relevant. However, ecologically important traits such as PE should also be investigated in order to achieve a more sustainable pig production while maintaining the same production level. Although FCR and RFI are expected to be correlated with PE, selection for improved FCR and RFI would likely increase energy efficiency rather than PE (Kasper et al., 2020a; Millet et al., 2018), since energy intake is the main factor driving feed intake. Moreover, it has been shown in poultry that selecting for improved FCR and RFI with the aim of reducing nutrient excretion may not be as efficient as selecting for the nutrient trait itself. de Verdal et al. (2011) reported that the selection for improved FCR and RFI in poultry is 19.3% and 53.4% less efficient, respectively, than selecting on the nutrient trait itself. Nevertheless, in contrast to FCR and RFI, very few studies have investigated the possibility to improve PE, which may be due to a number of factors such as difficulties in phenotyping animals for this trait and the lack of approved and validated proxies.

Previous studies using a range of pig breeds, growth phases and diets reported heritabilities between 36% and 43% for nitrogen retention (Saintilan et al., 2013). Heritabilities between 21% and 27% (Verschuren, 2021) as well as 36% and 42% (for carcass and empty body, respectively; (Kasper et al., 2020a) were presented for PE. Nitrogen digestibility coefficient, reflecting the pig's efficiency to digest dietary fiber and absorb proteins, had an estimated heritability of 27-56% (Déru et al., 2021). For total nitrogen excretion during the finisher phase, Shirali et al. (2014) reported a heritability (± SE) of 0.32 (± 0.21). Finally, several QTL for nitrogen excretion traits were mapped and their effects and genetic architecture were described (Shirali et al., 2013). All these studies indicate a potential to select for protein-efficient pigs.

To estimate PE, the amount of protein ingested as well as the amount of protein retained in the animal needs to be determined. While measuring the amount of protein ingested has been greatly facilitated with the use of automatic feeders that record daily feed intake of each pig, determining the amount of protein retention can be laborious and previously used methods are often not suitable for large-scale phenotyping. For instance, nitrogen retention can be predicted from lean meat content, which is estimated from the weights of primal cuts during dissection (Saintilan et al., 2013). The deuterium dilution technique enables the estimation of nitrogen excretion traits from empty body water content (Shirali et al., 2014). Nitrogen digestibility coefficient was estimated from near-infrared spectroscopy of feces (Déru et al., 2021). Protein efficiency can also be estimated from a range of parameters, such as feed intake and growth patterns (Verschuren, 2021). A direct, but expensive and laborious, method to determine PE is wet-chemistry analysis of the carcass and even the whole body, including blood and organs (Kasper et al., 2020a). Here, we use a novel phenotyping strategy including a dual-energy X-ray absorptiometry (DXA) device in combination with automated feeders to

estimate PE in a cheaper, more streamlined and faster, but still accurate way (Kasper et al., 2021).

The knowledge of genetic correlations of PE with other traits of importance (such as meat quality and performance traits) is also important in order to account for possible trade-offs with traits included in current breeding programs. Studies have reported both favourable and unfavourable genetic relationships between the commonly used feed efficiency traits (FCR and RFI) with meat quality traits and average daily gain (Saintilan et al., 2013; Shirali et al., 2012). Phosphorus efficiency and its genetic correlation with PE is also an important trait to consider, as the low N:P ratios in pig feces result in excess of phosphorus in soils when pig manure is used as a fertilizer (Wienhold, 2005; Zhang et al., 2021). In addition, it is necessary to assess whether, at least on a phenotypic basis, PE could be associated with customers' acceptance of meat based on flavor, tenderness and juiciness.

The major aim of this study was therefore to estimate the quantitative genetic parameters for PE and its genetic correlations with phosphorus efficiency, production and meat quality traits when dietary protein is reduced. In addition, we aim to estimate genetic parameters for performance traits (ADG, ADFI and FCR) and meat quality traits, and their genetic correlations. Finally, we evaluated differences in meat sensory analysis between different PE groups based on tenderness, flavor and juiciness.

Methods

Animals and data sets

A total of 1,071 pigs using combined datasets from previous experiments (Kasper et al., 2020a: 294 pigs; Bee et al., 2021: 48 pigs; 48 pigs in a further study on protein and essential amino-acid reduction in the growth and finisher period or solely in the finisher period; Bee et

al., unpublished; and an additional 681 pigs raised specifically for this study) were used in the analysis of PE (Table 1). In all experiments explained below, pigs had *ad libitum* access to isocaloric diets that differed in crude protein or fibre content. Furthermore, in all experiments, pigs were fed a grower diet from 20 to 60 kg body weight and a finisher diet from 60 to slaughter. In some experiments, pigs were kept until a target weight of 140 kg and fed a specially formulated finisher diet from 100 to 140 kg (Ruiz-Ascacibar et al., 2017). In all experiments, control diets were formulated according to the Swiss feeding recommendations for pigs (Agroscope 2017). The data from previous experiments at Agroscope (Kasper et al., 2020b) included four experimental runs with eight farrowing series, and pigs were assigned either to the control or protein-restricted diets. The protein-restricted diets contained 80% of the crude protein and digestible essential amino acids content of the respective control diets. The data collected by Bee et al. (2021) included two experimental runs and pigs were assigned to three experimental treatments (T95, T100, and T100-CF). Pigs in the T95 treatment were fed the control diets that complied with the BIOSUISSE regulation, which allows 95% of the feed ingredients being of organic origin (https://www.bio-suisse.ch/de/richtlinienweisungen.php). The diets in the T100 treatment consisted of 100% feed ingredients that complied with the aforementioned regulation. The diet used in the T100-CF treatment was the same formulation as the T100, but with the crude fibre content increased to 6% by including sunflower press cake, sainfoin and lupine. Pigs in this experiment were slaughtered at a target BW of 105 kg. The 48 pigs from the unpublished study were assigned to three experimental treatments: C, the control diet that contained 80% of the crude protein and digestible essential amino acids content of the respective control diet only in the finisher, but with the control diet in the grower phase (RPF), and another one with a protein reduction in both, grower and finisher phase (RPCF). Due to similarities between treatment groups in all experiments described above, treatment groups were pooled over different experiments (Table 1). Pigs were slaughtered at a target body weight of 100 kg.

Finally, the 681 pigs that were raised and phenotyped specifically for this study, originated from 14 farrowing series (39 sires and 79 dams in total), and data were collected from October 2018 to June 2021. Forty-eight dams had one litter, 23 dams had two litters and eight dams had three litters. All sires and dams were of the Swiss Large White breed. All pigs in this experiment were fed a RPCF diet. Pigs in this experiment were slaughtered at an average body weight of 106 ± 5 kg.

Piglets were weaned at an average age of 27 ± 2 days after birth by removing the sow and were fed a standard starter diet with crude protein levels following the recommendation (Agroscope 2017). At 22.3 (± 1.6) kg, pigs were placed in pens equipped with automatic feeders (single-spaced automatic feeder stations with individual pig recognition system by Schauer Maschinenfabrik GmbH & Co. KG, Prambachkirchen, Austria) and stayed on the starter diet. The experiment started at this stage and all pigs learned to access the automatic feeders, which allows monitoring of feed intake. The automatic feeder recorded all feeder visits and feed consumption per visit, from which the total feed intake of each pig was calculated (Ewaoluwagbemiga et al., 2021). Every week, pigs were weighed individually, and, once the pig reached the target start weight of 20 kg, they were allocated to grower-finisher pens and the experimental treatments were started. This was done until a maximum number of 12 (or 24 or 48) pigs per pen (depending on the pen layout; minimum 1m^2 per pig and maximum 12 pigs/feeder) was reached. Pigs remained in this pen until slaughter.

Total and average daily feed (ADFI) was recorded, and average daily gain (ADG) and the feed conversion ratio (FCR) were calculated as;

$$\mathrm{ADG} = \frac{\text{Slaughter weight} - \text{Weight at 20 kg}}{\text{Slaughter age} - \text{Age at 20 kg}}$$

$$\text{FCR} = \frac{\text{Average daily feed intake}}{\text{ADG}}$$

Table 1: Overview of datasets and the origin of the 1,071 pigs used in the study, indicating the differences in the number of animals, sexes, and methods to determine carcass protein content, treatment groups, dietary crude protein and digestible lysine content.

Study	Sex			Sires	Dams	Protein determination	T1[1]	T2[2]	Dietary raw protein (digestible lysine content (g/kg))[3]		
	Castrated male	Female	Entire male						Grower (20-60 kg BW)	Finisher I (60-100 kg BW)	Finisher II (100-140 kg BW)
Kasper et al. (2020)[4]	92	92	110	17	56	Chemical analysis	Control	Control A	163 (9.72)	140 (7.80)	124 (7.15)
							RPCF	Treatment A	134 (7.88)	115 (6.36)	101 (5.76)
Bee et al. (2021)[5]	24	24	-	3	9	DXA	T95	Control B	184 (11.04)	158 (8.49)	-
							T100	Control B	185 (10.96)	156 (8.71)	-
							T100-CF	Control C	185 (10.45)	156 (8.24)	-
Bee et al. (unpublished)	24	24	-	4	9	DXA	Control	Control A	164 (10.07)	152 (8.13)	-
							RPF	Treatment B	164 (10.07)	121 (6.56)	-
							RPCF	Treatment A	132 (8.13)	121 (6.56)	-
Present study	329	352	-	39	79	DXA	RPCF	Treatment A	128 (7.80)	112 (6.06)	-
Total	469	492	110								

[1]T1: name of treatment group in original study; RPCF: reduced protein diet in the grower and finisher stage; RPF: reduced protein diet in the finisher stage; T95: 95% of feed ingredients were of organic origin; T100: 100% of feed ingredients were of organic origin; T100-CF: 100% of feed ingredients of organic origin with 6% higher crude fiber content

[2]T2: newly assigned name of treatment group based on the quantity of dietary crude protein and crude fiber

[3]Energy content was the same (13.4 MJ) for both grower and finisher diet and for all experimental treatments

[4]RP content for the study of Kasper et al. (2020) was averaged over four series

[5]For the study of Bee et al. (2021), all treatment groups had approximately the same quantity of crude protein but T100-CF had a higher crude fiber content, hence, the different treatment group (Control C) assigned to T100-CF.

Protein and phosphorus efficiency

For the data in Kasper et al. (2020a), pigs were serially slaughtered at 20 – 140 kg body weight in 20 kg intervals and the nitrogen and phosphorus content of the carcasses was determined by wet chemical analysis following the protocol described by (Ruiz-Ascacibar et al., 2017). For the other data sets, pigs were slaughtered at an average body weight of 106 ± 5 kg and the left carcass half, including the whole head and the tail, was scanned with a Dual-energy x-ray absorptiometry (DXA; GE Lunar i-DXA, GE Medical Systems, Glattbrugg, Switzerland) to determine the lean tissue content. The lean tissue content and bone mass obtained from the DXA scans was used in the following prediction equation to estimate the protein content retained in the carcass (Kasper et al., 2021).

$$\boldsymbol{CP_{carcass}\ (g) = -482.745 + 0.23\ (Lean_{DXA}(\mathrm{g}) \times P)}$$

$$\boldsymbol{Ph_{carcass}\ (g) = -6.388 + 0.109\ (BMC_{DXA}(\mathrm{g}) \times P) + 0.004\ (Lean_{DXA}(\mathrm{g}) \times P)}$$

Where $CP_{carcass}\ (g)$ is the crude protein content of the carcass in g, $Lean_{DXA}(\mathrm{g})$ is the lean meat content obtained with DXA in g, P is the proportion of the weight of the left cold carcass-half weight (including the whole head and the tail) to the total cold carcass weight, $Ph_{carcass}\ (g)$ is the phosphorus content of the carcass in g, and $BMC_{DXA}(\mathrm{g})$ is the bone mineral content obtained with DXA in g. Protein and phosphorus efficiency of the carcass was thereafter calculated as the ratio of protein (or phosphorus) retained in the carcass (corrected for protein (or phosphorus) content in the carcass at a target live body weight of 20 kg, which is the start of the experiment and when feed intake was first monitored) to the total protein (or phosphorus) intake ($\boldsymbol{CP_{feed}\ intake}\ (\mathrm{g})$) during the experimental period.

$$\boldsymbol{protein\ efficiency = \frac{CP_{carcass}\ (g)\ slaughter - CP_{carcass}\ (g)\ start}{CP_{feed}\ intake\ (\mathrm{g})}}$$

The protein and phosphorus content of pigs at the start of this experiment $\boldsymbol{CP_{carcass}}$ $(\boldsymbol{g})$ $\boldsymbol{start}$ was estimated from a sample of 38 piglets (12 females, 12 castrated males and 14 entire males). These 38 piglets were slaughtered at an average of 20.98 ± 1.85 kg body weight in a previous experiment and their carcass protein content was chemically determined (Ruiz-Ascacibar et al., 2017). The average protein content per kg carcass for each sex (female, entire male, castrated male) was used to estimate $\boldsymbol{CP_{carcass}}$ $(\boldsymbol{g})$ $\boldsymbol{start}$ for pigs by multiplying the actual live body weight of pigs when they entered the experiment (i.e. at approximately 20 kg body weight) with the protein content per kg carcass of piglet, as previously determined from the 38 piglets (Ruiz-Ascacibar et al., 2017).

Meat quality traits and predictor variables in the study

In order to investigate possible trade-offs between PE and other traits of importance, such as meat quality and performance, additional traits were recorded on a subset of pigs raised specifically for this study (N=510; Table 2). After exsanguination and evisceration, backfat thickness was measured at the 10th rib level on the hot left carcass side with a ruler. Thereafter, the eviscerated carcasses (left and right half) were weighed and then stored overnight at 2 °C. One day after slaughter, the longissimus thoracii (LT) muscle was excised (at the 10th to 12th rib level) from the left cold carcass side. The area of the LT was measured at the 11th to 12th rib level. A 1x pixel JPEG image of the muscle was taken with a smartphone camera (always mounted on the same support structure to guarantee the same angle and distance to the object) together with a ruler for scale. Subsequently, the area was measured with the imageJ software (v1.53r). In addition, two 3-cm thick chops, labeled A and B, were cut. After a 20 min bloom period at 4°C, L* (lightness), a* (redness), and b* (yellowness) values for chop A were measured using a spectrophotometer (model CM-2600d, Minolta, Dietikon, Switzerland). Three replicated measurements were performed on each sample. Subsequently, from the same chop, drip loss was assessed as the quantity of purge generated

during storage at 4 °C for 24 h. Thereafter, the samples were vacuum-sealed in plastic bags and cooked in a water bath at 72 °C for 45 min, then cooled in cold water for 15 min, rinsed to remove coagulated sarcoplasmic protein, dabbed dry and weighed to determine the cooking loss. The cooked chops were then stored at -20 °C until measuring the shear force. Shear force was then determined on the cooked samples, which were slowly brought to ambient temperature. We measured shear force from five cores of each LT chop with a diameter of 1.27 cm perpendicular to the fiber direction using the Stable Micro System TA.XT2 Texture Analyzer (Godalming, Surry, UK) equipped with a 2.5-mm-thick Warner-Bratzler shear. The chops labeled B were freed from subcutaneous fat and then used for the determination of the intramuscular fat content. The samples were placed in plastic bags, vacuumed-sealed and frozen at -20 °C until analysis. The frozen samples were lyophilized using a Delta 2-24 machine (Christ Delta 2-24, Kühner AG, Birsfelden, Switzerland) and the intramuscular fat content was determined by extracting with petrol ether after an acid hydrolysis (International Organization for standardization (ISO), 1999).

Drip loss and cooking loss were calculated as;

$$\text{Drip Loss (DL)} = \frac{\text{Weight 1} - \text{Weight 2}}{\text{weight 1}}$$

$$\text{Cooking Loss (CL)} = \frac{\text{Weight 2} - \text{Weight 3}}{\text{weight 2}}$$

Predictor variables such as slaughter weight, slaughter age, treatment, year of change, sex and temperature were included in the genetic analysis of the efficiency traits, performance traits and meat quality traits. Slaughter weight is the weight of the animal at the time of slaughter and slaughter age is the age of the animal at slaughter. Due to high correlation of slaughter age with slaughter weight (Pearson r = 0.77, $p < 0.001$), we used the residuals of a linear regression of slaughter age on slaughter weight (rAgeLW) in place of slaughter age to avoid

collinearity. Year of change is the year the animal entered into the experiment at an average body weight of 20 kg. Temperature is the average ambient temperature (± 3 days) of barn at the time the animal entered into the experiment.

Table 2: Traits measured in addition to protein and phosphorus efficiency and predictor variables used in analysis

Variable category	Trait/variable
Nutrient efficiency (N=1,071)	Protein efficiency Phosphorus efficiency
Meat quality (N=510)	Meat colour (lightness, redness and yellowness) Intra-muscular fat content Water holding capacity (drip loss, cooking loss) Shear force Backfat thickness Loin muscle area
Sensory analysis of prepared meat (N=	Firmness Tenderness Juiciness Flavour
Performance traits (N=1,071)	Average daily gain (ADG) Feed conversion rate (FCR) Average daily feed intake (ADFI)
Predictor variables (N=1,071)	Temperature Sex Treatment Year of change Slaughter weight Slaughter age (rAgeLW; residuals of slaughter age on slaughter weight)

Sensory Analysis of Prepared Meat

The objective of the sensory analysis was to identify potential differences in the perceived initial firmness (first bite), tenderness, juiciness and flavour of meat samples between three groups differing in PE (low, LPE; medium, MPE; and high, HPE). Chops of 2 cm thickness were selected from pigs raised specifically for this study. Pigs with a PE less than the mean PE - 2σ were considered as LPE (group average PE of 0.35 ± 0.08), pigs with a PE greater

than mean PE + 2σ were considered as HPE (group average PE of 0.57± 0.05), and pigs in between were considered as MPE group (group average PE of 0.40 ± 0.01). A total number of 12 chops (from 6 castrates and 6 females), 13 chops (from 6 castrates and 7 females), and 12 chops (from 6 castrates and 8 females) were used in HPE, MPE, and LPE, respectively. Chops were taken between the 11th and 12th ribs (the same chop used in measuring loin muscle area) of the left cold carcass half 24h postmortem and stored at -80 °C. For the sensory analysis, chops were thawed for 24 h at 4°C, blotted dry and stored at room temperature for approximately 1h. Slices were grilled at 180 °C for 2.45 min on each side and cut into pieces of approximately 2 × 2 cm.

The chops differed in the thickness of the attached fat (<1.5 cm, 1.5 cm or 3 cm), which we corrected statistically in the model. The cut samples were kept at 60°C until sensory testing. A sensory panel of eight judges participated in the sensory tests. Intensity of the attributes firmness, tenderness, juiciness, and total flavour intensity was measured on an unstructured 10-cm line scale labelled form none (0) to high (10). Prior to data collection, panelists participated in two training sessions to get familiar with the attributes of interest. In each of the total six sessions, panelists evaluated two sample sets, each of them consisting of meat cuts of three different animals. Sample sets and samples within each test set were randomized according to a William Latin Square design. All samples were coded with three-digit random numbers. Sensory data were collected using the software FIZZ (version 2.51 Biosystèmes, Couternon, France). White bread, still water and warm black tea were provided for neutralisation of the mouth between samples. All tests were conducted at room temperature under day light conditions in the sensory laboratory at Agroscope Posieux.

Statistical analysis

All analysis were performed in R software V 4.2.1 (R Core Team, 2020). The *pedantics* package V 1.7 (Morrissey and Wilson, 2010) was used to construct a multigenerational pedigree for the animal model and to derive pedigree-based parameters such as relatedness and inbreeding. The total pedigree contained 1468 unique individuals with a maximum pedigree depth of 12 generations. From these individuals, 682 pigs were pigs raised specifically for this study, 390 pigs were from previous experiments (described in Kasper et al., 2020a; Bee et al., 2021 and Bee et al., unpublished), and 396 pigs with no phenotypes provided links for the individuals with PE data. All phenotyped individuals had both parents known. There was a mean inbreeding coefficient of 0.00032. The genetic analysis was performed using the Markov Chain Monte Carlo generalized linear mixed model (MCMCglmm) package V 2.33 (Hadfield, 2010). MCMCglmm gives a so-called Bayesian P-value (p_{MCMC}), which is twice the posterior probability that the parameter value is less than or greater than zero (the smaller one of the two possibilities is taken; (Hadfield, 2010). To determine the effect of several variables on PE, we first ran a linear model that included all those variables and interactions as fixed effects and sire and dam ID as random effects. We selected the top model(s), i.e. all models within delta AIC < 2 with the 'dredge' function in MuMin package V 1.46.0 (Bartoń, 2022). The variables retained in the top model were then used as fixed effects in the univariate animal model to estimate the genetic and common environmental variance components. The univariate models were performed using the model formula;

$$y = Xb + Z_a a + Z_c c + e$$

Where $\boldsymbol{y}$ is a vector of observations of the respective trait, $\boldsymbol{b}$ is a vector of fixed effects of the year the pig entered the experiment (year of change), slaughter weight, residuals of slaughter age on slaughter weight (rAgeLW), experimental treatment, sex, temperature, treatment × rAgeLW interaction, slaughter weight × sex interaction, treatment × sex interaction, and year

of change × rAgeLW interaction. $\boldsymbol{X}$ is an incidence matrix relating records to fixed effects, $\boldsymbol{a}$ is a vector of random additive genetic effects, and $\boldsymbol{Z}$ is the corresponding incidence matrix. $\boldsymbol{c}$ is a vector of random litter effects, and $\boldsymbol{Z_c}$ is the corresponding incidence matrix, and $\boldsymbol{e}$ is the random residual effect. Heritability was thereafter computed as the ratio of genetic variance to the phenotypic variance ($h^2 = V_A / V_P$), where phenotypic variance (V_P) is the sum of genetic variance (V_A), litter (common environmental) effect (V_{CE}) and residual variance (V_R). The litter effect was calculated as the ratio of litter effect to phenotypic variance ($CE^2 = V_{CE}/V_P$). A non-informative prior with an inverse Wishart distribution was used for the random effects and a normal distribution for the fixed effects. The inverse Wishart distribution for the random effects and residual variance had priors with variance parameter (V) of one and a degree-of-belief parameter (nu) of 0.002. The model was run with 2 million iterations, of which 100,000 were discarded as burn-in and the resulting posterior distribution was sampled at thinning intervals of 1,000. We performed the following diagnostics test to ensure model convergence. We first visually checked the trace plot to ensure that there was no upward or downward trend in the trace. We also checked the autocorrelation (<0.1) and the effective sample size, which is a measure of the size of uncorrelated sample chain, and should be >1,000. Finally, we performed the Heidelberg stationarity test of convergence, whose p-values must be greater than 0.05. The robustness of the estimates was checked by running the models an additional three times. In order to aid the assessment whether the posterior distributions of the respective effect are well separated from zero, we compared them with null distributions (random permutation of the variable vector; Kasper et al., 2020a; Araya-Ajoy and Dingemanse, 2017). Then, we computed the proportion of the real posterior distributions that were not overlapping with the random distribution (see Supplementary Information Figures S1 to S3).

Genetic correlations were estimated using bivariate models including the additive genetic and

common environment covariance, in which we added year, slaughter weight, treatment, sex, temperature, slaughter age (rAgeLW) as fixed effects. After encountering convergence issues with meat-quality models (probably due to the reduced sample size), we removed the common environment effect from those models. Weakly informative priors were used (V = diag(2)/2, nu = 2). The models were run with 3 million iterations, of which 100,000 were discarded as burn-in and the resulting posterior distribution was sampled at thinning intervals of 1,000. The quality of the models was checked analogously to the procedure described above for the univariate models. Genetic correlations were computed by rescaling additive genetic covariances by the variances. Correlations whose 95% credible intervals that did not include zero were considered as statistically distinct from zero.

While all data (N=1071) were used in the heritability estimation of PE and performance traits and their genetic correlations, heritability estimation of meat quality was done on a subset (N=510) for which these phenotypes were available. The univariate animal models used in the heritability estimation of meat quality traits did not contain the fixed effect of treatment since the subset for which meat quality measurements were available had only one treatment group. Initially, we included the random litter effect, but the models did not converge, most likely due to over-parameterization. Thus, we excluded the random litter effect, and the interactions differ between meat quality traits depending on the top model for each trait (Supplementary S1). Analogously, we did not include the litter effect in the bivariate models for meat quality traits.

A mixed-effects model was used for the phenotypic analysis of meat sensory data to correct for the effect of session and judge in the nlme package in R (Pinheiro et al., 2022), and Fisher's LSD mean separation test were performed for post-hoc analysis. The model used was;

$$Y_{ijk} = \mu + \text{Session} + \text{J} + \text{Sex} + \text{PE} + \text{FT} + \varepsilon_{ijk}$$

Where Y_{ijk} are the observations for the dependent variables (initial firmness, tenderness, juiciness and flavour), μ is the overall mean, *Session* is the random effect for session, *J* is the random effect for judge, *Sex* is the fixed effect of sex (castrates and females), *PE* is the fixed effect of PE group (HPE, LPE and MPE), and *FT* is the fixed effect of the thickness of fat adhering to meat slices.

Results

Influence of fixed effects on PE, phosphorus efficiency, FCR, ADG and ADFI

The descriptive statistics for the efficiency traits, FCR, ADG, and ADFI are presented in Table 3. Using the entire dataset (1,071 pigs), PE, phosphorus efficiency, FCR, ADG and ADFI had a mean of 0.39 ± 0.04, 0.43 ± 0.05, 2.67 ± 0.23, 0.85 ± 0.11, and 2.26 ± 0.31, respectively (Table 3). Slaughter weight, experimental treatments, sex, age (rAgeLW), and ambient temperature showed significant influence on PE ($p_{MCMC} < 0.05$; Table 4). PE of pigs decreased by 0.7%, 0.4% and 1.1% as the slaughter weight ($p_{MCMC} = 0.0005$), ambient temperature ($p_{MCMC} = 0.029$) and age (rAgeLW) ($p_{MCMC} = 0.0005$) increased, respectively. While pigs in Treatment B (i.e. pigs fed a reduced protein diet at the finishing stage) were not statistically different from pigs in control A (i.e. pigs fed the standard diet) ($p_{MCMC} = 0.37$), pigs in Treatment A, Control B, and Control C were statistically different from pigs in Control A ($p_{MCMC} < 0.05$). Pigs in Treatment A (i.e. pigs fed a reduced protein diet in the grower and finisher period) had 1.8% higher PE compared to pigs in control A ($p_{MCMC} = 0.0005$). Pigs in control B (i.e. pigs fed the organic diet with RP content higher than the control A) and control C (i.e. pigs fed the organic diet and crude fibre with RP content higher than the control A) had 4.3% and 5.8% lower PE compared to those in control A ($p_{MCMC} < 0.01$). Sex showed significant influence on PE, with females having 1.3% higher PE than the castrated males ($p_{MCMC} = 0.007$) and males having 1.8% higher PE than the castrated males ($p_{MCMC} = 0.001$).

For phosphorus efficiency, there was a significant influence of slaughter weight, ambient temperature, and age (rAgeLW), with pigs having 1.6% (p_{MCMC} = 0.0005), 0.8% (p_{MCMC} = 0.001) and 1.4% (p_{MCMC} = 0.0005) lower phosphorus efficiency as slaughter weight, ambient temperature and age (rAgeLW) increased, respectively (Table 4). Experimental treatments showed statistical influence on phosphorus efficiency, with treatment A, control B, and control C having 1.9% (p_{MCMC} = 0.008), 6.5% (p_{MCMC} = 0.007) and 8.3% (p_{MCMC} = 0.0005) lower phosphorus efficiency compared to control A, respectively (Table 4). Sex also showed some influence on phosphorus efficiency, with males having 2.4% higher PE compared to castrated males (p_{MCMC} = 0.02) (Table 4).

For FCR, there was a significant influence of slaughter weight, experimental treatments, sex and age (rAgeLW). Pigs had 17% increased FCR as the slaughter weight increases (p_{MCMC} = 0.0005) and 9% lower FCR as the age (rAgeLW) increased (p_{MCMC} = 0.0005). Pigs in Treatment A and Control C had 17% (p_{MCMC} = 0.0005) and 16% (p_{MCMC} = 0.04) increased FCR compared to pigs in Control A. Females and entire males had 7% (p_{MCMC} = 0.007) and 9.8% (p_{MCMC} = 0.002) lower FCR than the castrated males. For ADG and ADFI, there was a significant influence of year of change, slaughter weight, experimental treatments, sex and age (rAgeLW). ADG of pigs decreased by 2.3% as the slaughter weight increased (p_{MCMC} < 0.0005) and ADG increased by 9.1% as age (rAgeLW) increased (p_{MCMC} = 0.0005). Only pigs in Treatment A showed significant difference from pigs in control A for ADG (p_{MCMC} < 0.001), with pigs in Treatment A having 3.5% lower ADG compared to the pigs in control A. Castrated pigs were significantly different from females and entire males with females and entire males having lower ADG than the castrated males (p_{MCMC} < 0.01). Finally, ADFI increased as the slaughter weight and age (rAgeLW) increased (p_{MCMC} < 0.001). Only pigs in Treatment A showed a significant difference from pigs in control A for ADFI (p_{MCMC} < 0.01),

with pigs in Treatment A having higher ADFI compared to the pigs in control A. Castrated pigs were significantly different from females and entire males with females and entire males having lower ADFI compared to the castrated males ($p_{MCMC} < 0.01$).

Table 3: Descriptive statistics of traits for each study and the overall dataset

Trait	Study[1]	*N*	Mean	SD
Protein efficiency	Bee et al. (2021)	48	0.34	0.04
	Bee et al. (*unpublished*)	48	0.39	0.04
	Present study	681	0.40	0.03
	Overall[2]	1071	0.39	0.04
Phosphorus efficiency	Bee et al. (2021)	48	0.37	0.04
	Bee et al. (*unpublished*)	48	0.40	0.03
	Present study	681	0.42	0.03
	Overall[2]	1071	0.43	0.05
FCR	Bee et al. (2021)	48	2.54	0.15
	Bee et al. (*unpublished*)	48	2.59	0.11
	Present study	681	2.76	0.14
	Overall[2]	1071	2.67	0.23
ADG	Bee et al. (2021)	48	0.95	0.06
	Bee et al. (*unpublished*)	48	0.94	0.07
	Present study	681	0.84	0.11
	Overall[2]	1071	0.85	0.11
ADFI	Bee et al. (2021)	48	2.40	0.19
	Bee et al. (*unpublished*)	48	2.44	0.18
	Present study	681	2.32	0.26
	Overall[2]	1071	2.26	0.31

[1]Descriptive statistics for the data of Kasper et al. (2020) is in the study of Kasper et al. (2020)
[2]Descriptive statistics for "**Overall**" also includes the data from Kasper et al. (2020)

Table 4: Influence of fixed effects on efficiency and performance traits

		Protein efficiency		Phosphorus efficiency		FCR		ADG		ADFI	
Variable		**post. mean**	**p_{MCMC}**	**post. mean**	**p_{MCMC}**	**post. mean**	**p_{MCMC}**	**post. mean**	**p_{MCMC}**	**post. mean**	**p_{MCMC}**
Intercept		0.37	0.0005	0.43	0.0005	2.57	0.0005	0.88	0.0005	2.28	0.0005
Year		0.004	0.17	-0.001	0.80	0.019	0.11	0.013	0.009	0.044	0.002
Slaughter weight		-0.007	0.001	-0.016	0.0005	0.17	0.0005	-0.023	0.0005	0.085	0.0005
Treatment[1]	Control B	-0.043	0.003	-0.065	0.007	0.03	0.65	-0.0096	0.72	0.033	0.66
	Control C	-0.058	0.0005	-0.083	0.0005	0.16	0.04	-0.027	0.33	0.099	0.18
	Treatment A	0.018	0.0005	-0.019	0.008	0.17	0.0005	-0.035	0.0005	0.064	0.001
	Treatment B	0.016	0.37	-0.035	0.19	0.11	0.21	-0.017	0.58	0.069	0.39
Sex[2]	Females	0.013	0.007	0.0002	0.97	-0.07	0.007	-0.034	5×10^{-4}	-0.15	0.0005
	Males	0.018	0.001	0.024	0.02	-0.098	0.002	-0.031	0.005	-0.18	0.0005
Slaughter age (rAgeLW)		-0.011	0.0005	-0.014	0.0005	-0.09	0.0005	0.091	0.0005	0.18	0.0005
Temperature		-0.004	0.029	-0.008	0.001	0.003	0.68	0.0053	0.09	0.017	0.057

[1]Control A was included in the intercept

[2]Castrates was included in the intercept

Abbreviations: FCR (feed conversion ratio); ADG (average daily gain); ADFI (average daily feed intake)

Heritability and litter effects

The posterior distribution of the variance components of PE, phosphorus efficiency, FCR, ADG, and ADFI and their credible intervals are presented in Figure 1. Table 5 summarizes the estimates of heritabilities and variance components of PE and several performance and meat quality traits of Swiss Large White pigs. The result showed a heritability estimate (credible interval) of 0.43 (0.29, 0.58) for PE in the carcass. There was also a contribution of litter effect to the phenotypic variance in pigs' carcass for PE of 0.11 (0.07, 0.17), which showed that pigs in the same litter performed similarly compared to others in different litters, beyond the additive genetic effect. The heritability estimates of phosphorus efficiency, ADG, FCR, and ADFI were 0.36 (0.19, 0.54), 0.54 (0.39, 0.75), 0.46 (0.27, 0.63), and 0.61 (0.41, 0.83), respectively (Table 5). In addition, there was a litter effect of 0.12 (0.069, 0.16), 0.042 (0.014, 0.10), and 0.06 (0.023, 0.13) to ADG, FCR and ADFI, respectively. The heritability estimates of meat quality and carcass traits were moderate to high ranging from 0.31 (0.12, 0.61) in the LT area to 0.99 (0.58, 0.999) in intramuscular fat (Figure 2, Table 5). In general, heritabilities could be estimated with high levels of confidence, as reflected in the rather narrow credible intervals and the high proportion of non-overlap with null distributions (Table 5, Figures S1 and S3). In contrast, litter effects were much smaller and therefore closer to zero, resulting in higher overlap with the null distributions (Table 5, Figure S2).

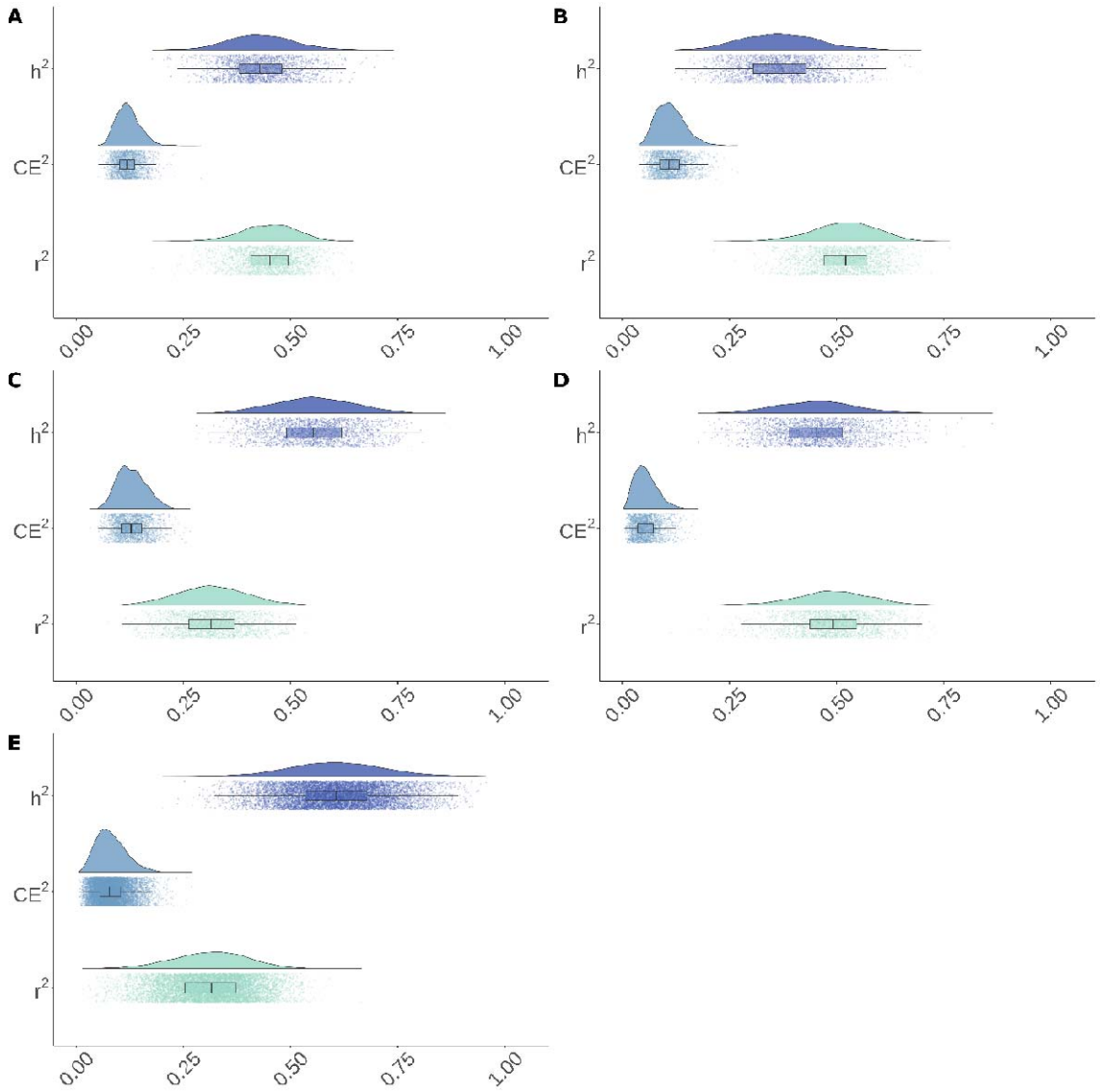

Figure 1: Heritability (h^2), common environment effect (CE^2) and residual variance (r^2) of protein efficiency (A), phosphorus efficiency (B), average daily gain (C), feed conversion ratio (D), and average daily feed intake (E). Posterior distributions of the respective variance components (upper part), points representing single estimates are shown together with a box plot (with median; whiskers represent the 95% credible interval).

Table 5: Estimates of additive genetic variance, heritability, common environment variance, litter effect and phenotypic variance of nutrient efficiency, performance, meat quality and carcass traits and their sample sizes. Credible intervals (95%) are given in parentheses. The percentage of non-overlap with a random distribution is displayed.

Trait	N	σ^2A	Heritability	% Non-overlap h^2	σ^2CE	Litter effect	% Non-overlap litter effect	σ^2P
PE	1071	5×10^{-4}(3×10^{-4}, 7×10^{-4})	0.43 (0.29 – 0.58)	99.98	1×10^{-4} (7×10^{-5}, 2×10^{-4})	0.12 (0.07, 0.17)	93.44	0.001 (0.00095, 0.0012)
PhE	1071	9×10^{-4}(4×10^{-4}, 0.001)	0.36 (0.19 – 0.54)	99.99	2×10^{-4}(1×10^{-4}, 4×10^{-4})	0.11 (0.06, 0.18)	95.81	0.002 (0.002, 0.003)
ADG	1071	0.002 (0.001, 0.003)	0.54 (0.39 – 0.75)	100	4×10^{-4} (2×10^{-4}, 6×10^{-4})	0.12 (0.07, 0.20)	99.85	0.003 (0.0029, 0.0037)
FCR	1071	0.01 (0.006, 0.016)	0.46 (0.27 – 0.63)	100	0.001 (3×10^{-4}, 0.003)	0.05 (0.01, 0.11)	88.13	0.024 (0.022, 0.027)
ADFI	1071	0.015 (0.009, 0.023)	0.61 (0.41 – 0.83)	100	0.002 (5×10^{-4}, 0.004)	0.07 (0.02, 0.15)	97.18	0.025 (0.022, 0.029)
L*	509	1.50 (0.66, 2.92)	0.32 (0.17 – 0.60)	99.97	-	-	-	4.66 (3.86, 5.25)
a*	509	0.48 (0.27, 0.81)	0.58 (0.37 – 0.83)	100	-	-	-	0.88 (0.73, 1.05)
b*	509	0.24 (0.13, 0.46)	0.37 (0.22 – 0.62)	99.98	-	-	-	0.62 (0.56, 0.76)
LMA	509	4.12 (1.40, 8.85)	0.31 (0.12 – 0.61)	99.06	-	-	-	13.56 (11.24, 15.91)
IMF	509	229 (105, 266)	0.99 (0.58 – 0.99)	100	-	-	-	229.09 (174.04, 259.98)
ShF	509	42.74 (17.80, 67.24)	0.43 (0.21 – 0.64)	99.94	-	-	-	95.23 (81.66, 111.12)
DL	509	0.51 (0.28, 0.99)	0.37 (0.21 – 0.59)	99.95	-	-	-	1.50 (1.34, 1.78)
CL	509	4.57 (2.70, 9.70)	0.38 (0.18 – 0.56)	99.97	-	-	-	15.97 (13.96, 18.51)
BT	509	8.99 (4.80, 15.02)	0.48 (0.30 – 0.72)	99.96	-	-	-	18.08 (15.5, 21.5)

Abbreviations: PE, protein efficiency; PhE, phosphorus efficiency; ADG, average daily gain; FCR, feed conversion ratio; ADFI, average daily feed intake; L*, meat lightness; a*, meat redness; b*, meat yellowness; LMA, loin muscle area; IMF, intramuscular fat; ShF, shear force; DL, drip loss; CL, cooking loss; BT, backfat thickness. N, sample size, σ^2A, additive genetic variance; σ^2CE, common environment variance; σ^2P, phenotypic variance.

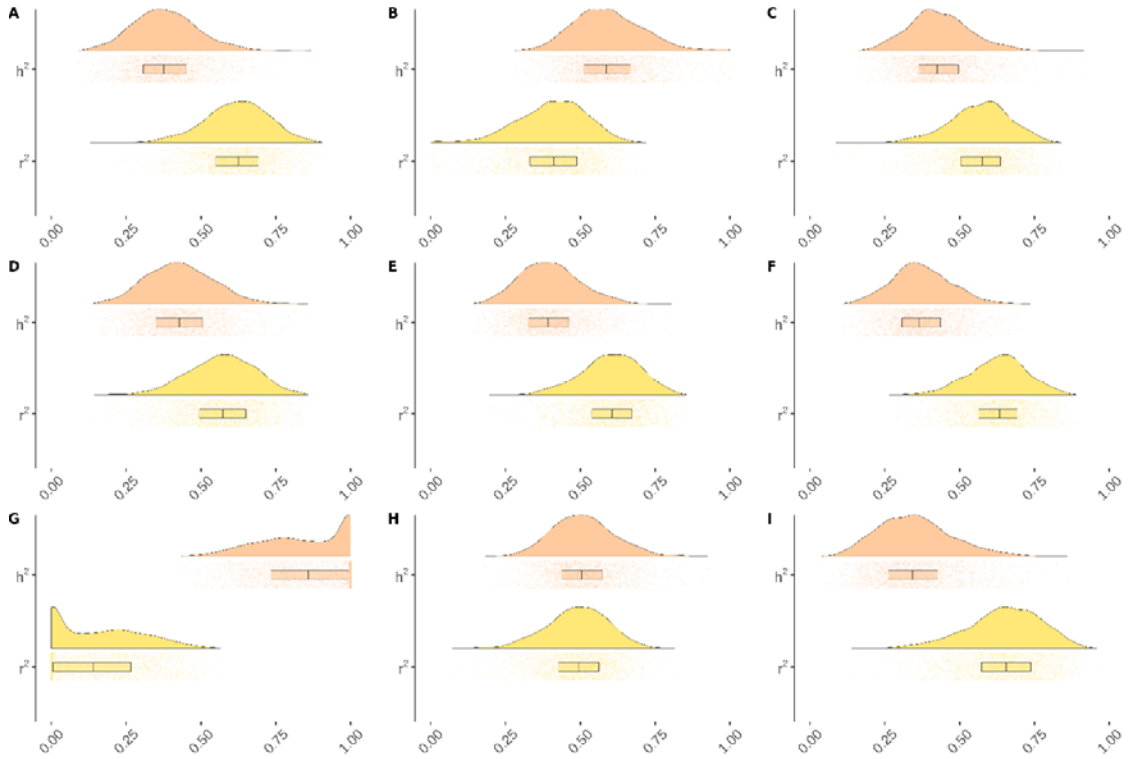

Figure 2: Heritability (h^2), common environment effect (CE^2) and residual variance (r^2) of meat lightness (A), meat redness (B), meat yellowness (C), shear force (D), drip loss (E), cooking loss (F), intramuscular fat content (G), backfat thickness (H), and loin muscle area (I). Posterior distributions of the respective variance components (upper part), points representing single estimates are shown together with a box plot (with median; whiskers represent the 95% credible interval).

Genetic and phenotypic correlations

Efficiency and performance traits

As PE is a new efficiency trait that is closer to the goal of sustainability, we sought to assess potential trade-offs with the traits commonly included in breeding goals, such as FCR and other performance traits. The genetic correlations between PE and performance traits were moderate and clearly different from zero. PE showed significant genetic correlations with phosphorus efficiency (0.12 [0.04 – 0.21]), ADFI (-0.61 [-0.69, -0.50]), FCR (-0.40 [-0.50, -0.30]) and ADG (-0.34 [-0.41, -0.23]) (Table 6). However, the phenotypic correlations of PE with performance traits were different from zero (ADFI (-0.96 [-0.97, -0.95]), FCR (-0.97 [-0.98, -0.97]) and ADG (-0.73 [-0.79, -0.67])) and higher than the genetic correlations (Table 6). While the relationship between PE and ADFI and FCR is favourable (i.e. pigs with higher

PE consume less feed and efficiently convert the feed), the relationship between PE and ADG is unfavourable (i.e. pigs with higher PE tend to grow slowly). FCR showed negative genetic correlations of -0.55 (-0.62, -0.42) and -0.41 (-0.54, -0.29) with ADG and ADFI, respectively (Table 6). Similar negative correlations were also observed for the phenotypic correlations of FCR with ADG and ADFI. However, the genetic correlation of FCR with ADFI was higher than its phenotypic correlation.

Efficiency and meat quality traits

The genetic correlations between PE and meat quality traits were not significantly different from zero, except for meat redness (a*) and meat yellowness (b*), which had potentially unfavourable negative genetic correlations with PE (-0.40 [-0.58, -0.09] and -0.27 [-0.45, -0.04], respectively) (Table 7). A similar pattern was also observed with the phenotypic correlations of PE with meat quality traits, where PE showed no significant phenotypic correlations with meat quality traits except for meat redness and meat yellowness (Table 7). However, the 95% credible intervals for the genetic and phenotypic correlations of PE with the r* and b* values were wide (Table 7). FCR showed unfavourable negative genetic correlations with meat colour (L* = -0.91 [-0.96, -0.67]) and a* = -0.25 [-0.43, -0.005]) and drip loss (-0.20 [-0.37, -0.05]) and cooking loss (-0.45 [-0.66, -0.14]) (Table 8). Phenotypic correlations of FCR with meat colour and water holding capacity were similar, except for the a* values, where it's the phenotypic correlation with FCR was not different from zero (Table 8). However, both the genetic and phenotypic correlations of FCR with meat colour and water holding capacity also had wide credible intervals except for FCR with meat lightness.

Table 6: Estimates of genetic correlations (above diagonals) and phenotypic correlations (below diagonals) between protein efficiency and performance traits with their 95% credible intervals in parentheses. Estimates, whose credible intervals do not span zero, are printed in bold.

	PE	PhE	ADG	FCR	ADFI
PE		**0.12 (0.03, 0.21)**	**-0.34 (-0.41, -0.23)**	**-0.40 (-0.50, -0.30)**	**-0.61 (-0.69, -0.50)**
PhE	0.07 (-0.03, 0.16)		**-0.36 (-0.46, -0.28)**	**-0.42 (-0.51, -0.30)**	**-0.63 (-0.70, -0.51)**
ADG	**-0.73 (-0.79, -0.67)**	**-0.36 (-0.46, -0.28)**		**-0.55 (-0.62, -0.42)**	-0.07 (-0.21, 0.05)
FCR	**-0.97 (-0.98, -0.97)**	**-0.98 (-0.98, -0.97)**	**-0.97 (-0.98, -0.96)**		**-0.41 (-0.54, -0.29)**
ADFI	**-0.96 (-0.97, -0.95)**	**-0.96 (-0.97, -0.95)**	**-0.90 (-0.93, -0.83)**	**-0.29 (-0.35, -0.21)**	

Abbreviations: PE, protein efficiency; PhE, phosphorus efficiency; ADG, average daily gain; FCR, feed conversion ratio; ADFI, average daily feed intake

Table 7: Estimates of genetic correlations (above diagonals) and phenotypic correlations (below diagonals) between protein efficiency and meat quality traits with their 95% credible intervals in parentheses. Estimates, whose credible intervals do not span zero, are printed in bold.

	PE	**L***	**a***	**b***	**LMA**	**IMF**	**ShF**	**DL**	**CL**	**BT**
PE		-0.62 (-0.87, 0.42)	**-0.40 (-0.58, -0.09)**	**-0.27 (-0.45, -0.04)**	-0.01 (-0.21, 0.19)	-0.09 (-0.29, 0.10)	-0.006 (-0.25, 0.23)	0.05 (-0.14, 0.18)	-0.13 (-0.34, 0.38)	-0.18 (-0.42, 0.08)
L*	-0.44 (-0.75, 0.36)		**-0.91 (-0.96, -0.73)**	**0.98 (-0.94, -0.99)**	**-0.63 (-0.78, -0.41)**	**0.48 (0.14, 0.66)**	**-0.87 (-0.94, -0.71)**	**-0.98 (-0.99, -0.97)**	**-0.77 (-0.86, -0.60)**	**-0.82 (-0.92, -0.72)**
a*	**-0.31 (-0.48, -0.07)**	**-0.85 (-0.91, -0.65)**		0.02 (-0.17, 0.31)	**-0.64 (-0.78, -0.49)**	**0.38 (0.17, 0.53)**	**-0.73 (-0.83, -0.61)**	**-0.58 (-0.75, -0.40)**	**-0.78 (-0.88, -0.62)**	-0.12 (-0.39, 0.08)
b*	**-0.21 (-0.35, -0.03)**	**0.95 (0.89, 0.98)**	**0.29 (0.19, 0.40)**		**-0.70 (-0.80, -0.43)**	**0.62 (0.44, 0.78)**	**-0.91 (-0.94, -0.84)**	**-0.45 (-0.67, -0.12)**	**-0.84 (-0.90, -0.67)**	-0.14 (-0.43, 0.15)
LMA	0.009 (-0.16, 0.14)	**-0.42 (-0.57, -0.33)**	**-0.55 (-0.65, -0.40)**	**-0.53 (-0.66, -0.34)**		**-0.31 (-0.71, -0.24)**	**-0.69 (-0.91, -0.22)**	**-0.21 (-0.49, -0.10)**	**0.94 (0.67, 0.99)**	**-0.66 (-0.84, -0.44)**
IMF	-0.07 (-0.22, 0.08)	**0.31 (0.18, 0.41)**	**0.28 (0.14, 0.40)**	**0.43 (0.31, 0.56)**	**-0.23 (-0.36, -0.09)**		**-0.52 (-0.73, -0.09)**	**-0.52 (-0.69, -0.27)**	**-0.43 (-0.71, -0.09)**	-0.15 (-0.38, 0.13)
ShF	0.015 (-0.19, 0.17)	**-0.72 (-0.78, -0.65)**	**-0.61 (-0.69, -0.52)**	**-0.79 (-0.83, -0.73)**	**-0.21 (-0.36, -0.07)**	**-0.34 (-0.45, -0.19)**		-0.27 (-0.54, 0.07)	-0.28 (-0.66, 0.18)	**-0.62 (-0.78, -0.46)**
DL	0.04 (-0.10, 0.14)	**-0.95 (-0.96, -0.94)**	**-0.34 (-0.43, -0.24)**	**-0.14 (-0.26, -0.04)**	-0.12 (-0.31, 0.09)	**-0.33 (-0.44, -0.18)**	-0.16 (-0.32, 0.03)		**0.48 (0.13, 0.78)**	**-0.63 (-0.82, -0.42)**
CL	-0.01 $ (-0.26, 0.29)	**-0.57 (-0.65, -0.48)**	**-0.65 (-0.73, -0.52)**	**-0.66 (-0.75, -0.52)**	**0.41 (0.32, 0.52)**	**-0.28 (-0.39, -0.15)**	0.01 (-0.12, 0.17)	**0.41 (0.13, 0.61)**		**-0.71 (-0.81, -0.55)**
BT	-0.14 (-0.33, 0.06)	**-0.67 (-0.74, -0.57)**	-0.08 (-0.25, 0.07)	-0.08 (-0.26, 0.10)	**-0.45 (-0.54, -0.34)**	0.01 (-0.12, 0.12)	**-0.47 (-0.57, -0.37)**	**-0.42 (-0.55, -0.27)**	**-0.52 (-0.58, -0.43)**	

Abbreviations: PE, protein efficiency; L*, meat lightness; a*, meat redness; b*, meat yellowness; LMA, loin muscle area; IMF, intramuscular fat; ShF, shear force; DL, drip loss; CL, cooking loss; BT, backfat thickness.

Table 8: Estimates of genetic correlations and phenotypic correlations between performance traits and meat quality and carcass traits with their 95% credible intervals in parentheses. Estimates, whose credible intervals do not span zero are printed in bold.

Genetic correlations

	L*	a*	b*	LMA	IMF	ShF	DL	CL	BT
ADG	-0.42 (-0.81, 0.57)	-0.12 (-0.38, 0.20)	-0.05 (-0.25, 0.17)	-0.04 (-0.26, 0.14)	0.16 (-0.01, 0.36))	-0.12 (-0.31, 0.17)	-0.07 (-0.20, 0.11)	-0.33 (-0.56, 0.067)	**0.31** **(0.04, 0.50)**
FCR	**-0.91** **(-0.96, -0.67)**	**-0.25** **(-0.43, -0.005)**	-0.12 (-0.28, 0.05)	-0.16 (-0.39, 0.12)	0.08 (-0.10, 0.28)	-0.03 (-0.22, 0.25)	**-0.20** **(-0.37, -0.05)**	**-0.45** **(-0.66, -0.14)**	0.07 (-0.15, 0.34)
ADFI	**-0.78** **(-0.91, -0.06)**	-0.002 (-0.25, 0.21)	0.07 (-0.12, 0.21)	**-0.27** **(-0.44, -0.016)**	**0.39** **(0.23, 0.54)**	-0.16 (-0.37, 0.07)	**-0.22** **(-0.35, -0.05)**	**-0.62** **(-0.76, -0.39)**	**0.55** **(0.36, 0.69)**

Phenotypic correlations

	L*	a*	b*	LMA	IMF	ShF	DL	CL	BT
ADG	-0.23 (-0.71, 0.57)	-0.08 (-0.29, 0.15)	-0.06 (-0.19, 0.12)	-0.03 (-0.20, 0.11)	0.12 (-0.01, 0.28)	-0.05 (-0.24, 0.13)	-0.04 (-0.15, 0.09)	-0.26 (-0.47, 0.04)	**0.20** **(0.03, 0.39)**
FCR	**-0.82** **(-0.92, -0.54)**	-0.14 (-0.32, 0.002)	-0.09 (-0.21, 0.02)	-0.12 (-0.30. 0.09)	0.08 (-0.07, 0.22)	-0.02 (-0.16, 0.19)	**-0.20** **(-0.30, -0.10)**	**-0.36** **(-0.55, -0.12)**	0.12 (-0.12, 0.25)
ADFI	**-0.69** **(-0.85, -0.04)**	-0.0009 (-0.19, 0.16)	0.05 (-0.08, 0.15)	**-0.16** **(-0.35, -0.014)**	**0.29** **(0.17, 0.43)**	-0.11 (-0.28, 0.06)	**-0.18** **(-0.26, -0.06)**	**-0.52** **(-0.66, -0.31)**	**0.43** **(0.28, 0.57)**

Abbreviations: ADG, average daily gain; FCR, feed conversion ratio; ADFI, average daily feed intake; L*, meat lightness; a*, meat redness; b*, meat yellowness; LMA, loin muscle area; IMF, intramuscular fat; ShF, shear force; DL, drip loss; CL, cooking loss; BT, backfat thickness

Sensory analysis

The results showed significant influence of judge and session on all the sensory attributes ($P < 0.01$), except for the influence of session on juiciness. A significant influence of PE group on juiciness could be observed ($P < 0.01$). However, MPE and LPE were not significantly different for juiciness, but a significant difference was observed between LPE and HPE as well as between MPE and HPE. This means that judges graded the juiciness of LPE and MPE meat samples equally, while they graded HPE samples as less juicy. Protein efficiency group did not show significant influence on initial firmness, tenderness and flavor ($P > 0.05$), suggesting that an improvement in PE may not influence the sensory attributes considered in this study except for juiciness. However, our results should be followed-up with a consumer panel to investigate whether consumers perceive the meat of the distinct PE groups as different.

Discussion

In this study, we estimated the heritability of PE, phosphorus efficiency and a range of performance and meat quality traits and their genetic correlations in a population of Swiss Large White pigs under various levels of dietary protein and amino acid supply. As already suggested previously (Kasper et al., 2020), we now clearly show a major potential of selecting protein efficient pigs, mostly without any apparent expected negative impact on production, meat quality and carcass traits. The analysis of the influence of environmental shows that PE is also influenced by ambient temperature, protein content of the feed, sex and age. Therefore, in addition to selection, there are various management practices that can be used to improve PE.

Protein and phosphorus efficiency

Similar to the study of (Kasper et al., 2020a) and (Ruiz-Ascacibar et al., 2017), this study also found an effect of treatment group (diet), sex and slaughter weight on protein and phosphorus efficiency. The heritability estimate reported in this study was slightly higher than that reported previously for the same population (Kasper et al., 2020a), which may be due to the higher sample size of the current study, in which the previous data was integrated. It is interesting to note that the heritability estimate of pigs using only the 681 pigs raised specifically for this study, which were fed reduced-protein diet in the growing and finishing phase was similar to the overall result (0.41 [0.22, 0.59] vs. 0.43 [0.29, 0.58]). Although only few studies have investigated PE in pigs, some have probed similar nutrient efficiency traits, such as total nitrogen excretion and nitrogen digestibility coefficient, and have reported varying heritabilities depending on the breed, growth phase, and diet (Verschuren, 2021; Saintilan et al., 2013; Déru et al., 2021; Shirali et al., 2014).

Our study showed a higher heritability for PE compared to most of the previous studies. These slight differences could be due to differences in breed and diet, but also to differences in the methods of nutrient efficiency estimation, which, in our case, might be more reliable compared to the use of indirect estimation methods, such as the deuterium technique or the estimation from lean meat content from dissections or production parameters. Consistent with previous work, the present study confirms that nutrient efficiency traits are heritable and can be harnessed to substantially reduce environmental pollution in pig production. However, in the practical implementation of breeding, it should be kept in mind that PE as a ratio trait may have a disadvantage. As argued by Zetouni et al. (2017), direct selection for a ratio trait such as PE may not lead to the desired result, as it is not certain whether the improvement comes from the counter trait (e.g. protein retention), the denominator trait (e.g. protein intake), or both. Therefore, it is advisable to use a multi-trait selection approach (i.e. selecting for both protein retention and protein intake) to achieve the highest genetic gain for a ratio trait

(Zetouni et al., 2017). In addition to direct genetic effects, the composition of the gut microbiome has been shown to influence general feed efficiency (Bergamaschi et al., 2020) and the genetic make-up of the host together with the composition of the microbiome explains more of the phenotypic variation in digestive efficiency of nitrogen than additive genetic variation alone (Déru et al., 2021). Thus, this important source of phenotypic variation should potentially be considered in breeding programs. However, gut microbiome analysis was beyond the scope of this study.

Performance traits

This study reports an influence of slaughter weight, sex and treatment group on average daily gain (ADG), feed conversion ratio (FCR) and average daily feed intake (ADFI), which is similar to the results of Kasper et al. (2020a) and Ruiz-Ascacibar et al. (2017). The heritabilities for performance traits were also mostly in line with those of other studies. We found a moderate heritabilities for ADG and ADFI, with ADG having lower heritability than that reported by (Shirali et al., 2014) of 0.64 ± 0.19. However, they were higher than the estimates reported by (Verschuren, 2021) (h^2 = 0.27 and h^2 = 0.43 for ADG and ADFI, respectively) and (Kavlak and Uimari, 2019) (h^2 = 0.25 ± 0.06 for ADG). FCR was also clearly heritable in the present study (h^2 = 0.46), which is similar to, although slightly higher than, the estimates reported by Saintilan et al. (2013). In contrast, Shirali et al. (2014) reported a lower heritability of 0.26 ± 0.20 over a period of 60 – 140 kg body weight. Previously, we also reported very low heritability estimates for FCR and ADG (Kasper et al., 2020a). These differing estimates compared to the present study could be due to the higher sample size in the present study, in which there were an additional 777 individuals available. Heritability for FCR may differ depending on growth phase and test period (e.g. at only the grower or finisher phase or throughout all growth phases) as reported by some studies where multiple QTLs for ADG and for FCR at different growth phases (Shirali et al., 2013; Silva et al., 2019; Reyer et

al., 2017). Our heritability estimates for meat quality traits are similar to those reported by Shirali et al. (2014), (Lo et al. (1992), Miar et al. (2014) and Lee et al. (2015). As in our study, the redness of the meat consistently showed higher heritability than the lightness and yellowness of the meat.

Genetic and phenotypic correlations with performance traits

Favourable genetic correlations were observed between PE and phosphorus efficiency as well as FCR and ADFI. This result shows that selection for increased PE would result in pigs that are also more phosphorus-efficient, consume less feed and efficiently convert the feed into body (and in particular muscle) mass. We observed an unfavourable relationship between PE and ADG, showing that selection for increased PE would likely result in pigs growing slower and would need to be countered accordingly. Similar relationships were found in the work of (Déru et al., 2021) on nitrogen digestible coefficient and of (Verschuren, 2021) on PE. In the latter study, the genetic relationships of PE with ADG, FCR and ADFI became stronger with growth phases. This suggests that the genetic factors underlying these traits and their covariances may vary across growth phases. Considering ecological footprint and feed costs, a focus on the finishing phase would therefore be more relevant, as the majority of feed is consumed in this period. The reason for the unfavourable relationship found between PE and ADG may be due to an indirect effect of lower feed intake since there is a negative relationship between PE and ADFI. However, the relationship observed between PE and ADG may not be linear; i.e. protein-efficient pigs do not necessarily grow slower during each growth phase. For example, Verschuren (2021) reported a low positive, i.e. favourable, genetic relationship (r_G = 0.11) between PE and ADG in the starter phase, but a low negative (r_G = -0.11) in the grower phase as well as a stronger, unfavourable relationship (r_G = -0.43) in the finisher phase. Furthermore, Shirali et al. (2013) also found QTLs for nitrogen excretion to be unfavourably associated with ADG only during the 90 kg to 120 kg body weight growth phase. Saintilan et al. (2013) also reported favourable genetic correlations of nitrogen

excretion efficiency with ADG, FCR and ADFI, but the one with FCR was close to 1, in contrast to r_G = -0.40 in our study. The reason for some of the discrepancy observed between this study and that of Saintilan et al. (2013) may be due to differences in methodology, traits, and sample size, but most importantly probably due to the mixing of growth phases. Estimation of the genetic correlation of PE and FCR on a subset of the whole data set, the part collected in the course of the current study, yielded a much higher value, namely r_G = -0.96 (-0.97, -0.95).

Genetic and phenotypic correlations with meat quality traits

In this study, we do not find significant genetic correlations of PE with most meat quality and carcass traits, indicating that selection for increased PE will likely not affect pork quality. However, the genetic correlations of PE with meat redness and yellowness were moderate, but clearly different from zero. This indicates that genetic improvement of PE might reduce the redness and yellowness of the meat (the meat might look paler), which could be perceived as unattractive by consumers. However, this may depend on the starting value of the meat colour. Déru et al. (2021) reported non-significant genetic correlations of nitrogen digestible coefficient with meat lightness, redness and yellowness, which were in an unfavourable direction for meat lightness and redness depending on the type of diet (conventional or high fiber diet). Since the credible intervals in our study were rather wide and reached close to zero, and the results of other studies are inconclusive, more data is required to ascertain this relationship. Moreover, additional experiments, such as the visual assessment and preferences of meat colour by consumers, should be conducted to investigate whether differences in meat colour within the expected range would lead to different consumer decisions. The sensory analysis in our study suggests no apparent conflicts of PE with the way the judges perceived the initial firmness, tenderness and flavor of the meat of a small subset of samples. However, the trained judges perceived the meat from highly protein-efficient pigs as less juicy than

from pigs that had average or below-average PE, but this effect has yet to be validated with a consumer panel.

The genetic correlations of FCR show possible unfavourable relationships with meat lightness, drip loss and cooking loss, which suggest that a selection for lower FCR in Swiss Large White pigs leads to lighter meat with reduced water holding capacity. This agrees with the study of Saintilan et al. (2013) who reported significant negative genetic correlations between FCR and meat lightness for Large White dam and sire breed.

Conclusions

Our results showed that PE is clearly heritable, and breeding for protein-efficient pigs is possible. It should be noted that the genetic parameters of PE were estimated here predominantly under conditions of low dietary protein availability. Together with the phenotypic results of the influence of diet presented in this work, and the still not resolved question of genotype-by-diet interactions, this shows the importance of the dietary environment and the influence of dietary protein content should be considered accordingly. The potential for coselecting improved phosphorus efficiency is small, since the genetic correlation of PE and phosphorus efficiency is rather low, but clearly distinct from zero. The lack of genetic correlations with meat quality and carcass traits indicates that no major conflicts will arise during selection, except for meat redness and yellowness, which might have to be closely monitored. As for production traits, genetic correlations are favourable except for average daily gain, which indicates that selection for increased protein efficiency might lead to slower growth. To achieve significant reduction in pollutant levels in manure, selection on conventional efficiency traits, such as FCR or RFI alone, might not be sufficient. Furthermore, we show that FCR showed genetic antagonism with meat quality traits in the

population studied. Thus, the inclusion of protein efficiency into current breeding goal would contribute better to a sustainable and environmentally friendly pig production.

Declarations

Ethics approval and consent to participate

The experimental procedure was approved by the Office for Food Safety and Veterinary Affairs (2018_30_FR) and all procedures were conducted in accordance with the Ordinance on Animal Protection and the Ordinance on Animal Experimentation.

Consent for publication

Not applicable

Availability of data and materials

The data that support the findings of this study and the code used for models and the statistical analysis are publicly available in Zenodo (DOI:10.5281/zenodo.6985500)

Competing interests

The authors report no conflicts of interest with any of the data presented.

Funding

This research was supported by the Fondation Sur-la-Croix to G.B. and C.K.

Authors' contributions

Conceptualization: E.E., G.B. and C.K. Data Curation: E.E. Formal Analysis: E.E. Funding Acquisition: G.B. and C.K. Methodology: E.E. and C.K. Project Administration: C.K. Software: E.E. Supervision: C.K. Visualization: E.E. Writing - Original Draft Preparation: E.E. Writing - Review & Editing: E.E., G.B. and C.K.

Acknowledgements

We are grateful to Guy Maïkoff and his team for the maintenance and slaughter of the pigs, for feed production and assistance with DXA scans and Marion Girard for the formulation of

the protein-reduced diet. Patrick Schlegel also provided help with the DXA scans. Sébastien Dubois and Paolo Silacci and their teams conducted the chemical analyses of feed and meat and helped with the collection of technological meat quality data, for which Martin Scheeder from Suisag shared protocols with us. Our thanks also go to Barbara Guggenbühl and her team for carrying out the sensory analysis, and Markus Neuditschko for comments on the manuscript.

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