Genetic determinism of boar taint in the French Landrace pig breed

C. Larzul*[1], M.-J. Mercat[2], C. Hassenfratz[2], C. Carillier-Jacquin[1], R. Comte[3], B. Blanchet[4], I. Louveau[3], S. Boulot[2], A. Prunier[3]

[1]Université de Toulouse, INRAE, ENVT, GenPhySE, 24 chemin de Borde-Rouge, 31326 Castanet-Tolosan, France;[2]IFIP-Institut du porc, Alliance R&D, La Motte au Vicomte, BP 35104, 35651 Le Rheu, France;[3]PEGASE, INRAE, Institut Agro, 16 Le Clos, 35590 Saint-Gilles, France ; [4]INRAE UE3P, 16 Le Clos, 35590 Saint-Gilles, France;
*catherine.larzul@inrae.fr

Abstract
Since pig breeds differ in their risk of developing boar taint, it is important to consider line-by-line selection by estimating genetic parameters of odorant compounds in relation to sexual development and production traits. The present study focused on French Landrace, one of the main French maternal lines. More than 1000 non-castrated males were measured for growth rate, body composition and meat quality, fat-odorant compounds, androstenone and skatole, and four steroid hormones. As expected, heritability values were high for androstenone (h^2=0.69) and estradiol (h^2=0.79). Genetic correlations of boar taint compounds were moderate to high with testosterone and estradiol but close to 0 with progesterone and cortisol. Genetic correlations of these compounds were low with growth rate, ultimate pH or color, but moderate and favorable with carcass leanness. It is therefore possible to include fat-odorant compounds in selection objectives, either directly or via sex hormones, while controlling their impacts on production performance.

Introduction
In France, male piglet castration without anaesthesia has been prohibited since January 1st, 2022. One of the primary motivations for castration of male pigs is to improve the quality of the meat, mainly to prevent the appearance of an odor defect known as boar taint. The two main components responsible for this defect are skatole (produced by bacteria in the digestive tract) and androstenone (a steroid produced by testes) which accumulate in fatty tissue. Reducing the level of these two compounds largely resolves the occurrence of the defect.
To promote the breeding of uncastrated male pigs, several pig lines have been developed under the label "low boar taint" (Larzul, 2021). Most of the effort has focused on the paternal lines. However, the influence of maternal lines should not be overlooked. In that respect, maternal lines are more at risk than paternal lines (Larzul, 2021). Specifying the genetic determinism of boar taint compounds in maternal lines is therefore an essential prerequisite for implementing selection strategies aimed at limiting boar taint without penalizing production traits. We estimated the genetic parameters of the boar taint compounds, in relation with growth, feed efficiency, body composition and meat. Steroid hormones have also been included in the study in order to clarify the genetic relationships between boar taint and testicular and adrenal metabolism and, possibly, to propose alternative selection criteria to reduce the risk of boar taint.

Materials & Methods

Animals. Between two and three weeks of age, male French Landrace piglets were transferred from their birth farm to the Rheu phenotyping station in 14 piglet post-weaning pens (UE3P,

https://doi.org/10.15454/1.5573932732039927E12). Around 26 kg, all the pigs of the pen were simultaneously transferred to the fattening pens to start the control at 35 kg live weight. The animals were slaughtered at the Cooperl Arc Atlantique slaughterhouse (Montfort, 35). At slaughter, the average body weight was 117 ± 6 kg, for a median age of 168 days. During the control period, the pigs were fed ad libitum with a feed with a net energy content (NE) of 9.6 MJ / kg, digestible lysine content of 0.94 g / MJ EN, and of digestible tryptophan of 1.7 g / kg. A total of 1084 animals, from 249 sires, were bred in 33 batches between June 2018 and April 2021.

Measures. The average daily gain (ADG) was calculated from the weights at the start and at the end of the control period. The feed conversion ratio (FCR) and the average daily feed intake (DFI) were calculated from the consumption recorded by the feeding device. A day before departure to the slaughterhouse, a blood sample was collected in heparinized tubes from the jugular vein. The blood samples were then centrifuged and the plasma was stored at -20 ° C until the concentrations of testosterone, estradiol, progesterone and cortisol were measured. Concentrations were measured using ELISA kits (ST AIA-Pack Testosterone, ST AIA-Pack hsE2, ST AIA-Pack CORT, ST AIA-PackPROGIII, Tosoh Corporation, Tokyo, Japan) developed for an automatic analyzer (AIATosoh Corporation, Tokyo, Japan). Dressing percentage (DY) is the ratio between the weight of the carcass with head 24 hours after slaughter and the weight before departure to the slaughterhouse after fasting. Carcass leanness (%M) was automatically estimated at the slaughterhouse (CSB Image-Meater®). The pH was measured (Sydel pHmeter, Xerolyt electrode) in the semimembranous muscle 24 hours post mortem (pH24). The day after slaughter, the colour parameters (L*a*b*) were measured (Minolta CR300 chromameter) on a fresh section of the *gluteus superficialis*. Finally, a sample of backfat was taken from the neck and frozen for subsequent determination of androstenone and skatole (Batorek et al., 2012).

Statistical analyses. Androstenone and skatole contents lower than 0.2 µg/g and 0.03 µg/g, respectively, can't be precisely measured. All values below these thresholds have been brought back to the threshold values. To normalize the distributions, the measurements obtained from the assays were transformed before analysis with the log function, except for the measurement of testosterone (square root transformation). All variables were then reduced and centered. For the dosages and the meat quality characteristics, the model included the effect of the weight at the end of the control period and the date of slaughter, equivalent to the batch of measurement. For the growth and food consumption traits, the model included the weight at the start of the control, the batch effect and the fattening pen as a random effect. For body composition measurements, the model took into account the weight before departure and the batch effect. The animal effect was added as a random effect in order to estimate the additive genetic variance. Six generations were considered to build the kindship matrix. The analyses were carried out with the VCE6 software (Neumaier and Groeneveld, 1998). Estimates of the variance components were performed jointly for the six assays. Other genetic correlations were estimated by two-trait analyses including one of the traits obtained from the assays and one of the other traits.

Results

The estimated heritabilities for these traits are all moderate to high. The highest heritabilities are observed for plasma estradiol level (h^2 = 0.80) and androstenone level in back fat (h^2= 0.83). The lowest heritabilities were observed for the level of testosterone (h^2=0.26) and progesterone (h^2=0.34). The estimated heritabilities for cortisol (h^2 = 0.54) and skatole (h^2=

0.50) were medium. The genetic correlations between compounds and production traits are reported in Table 1.

Table 1. Genetic correlations between boar taint compounds, steroid hormones and production traits.

	Es	Pr	Co	An	Sk	ADG	FCR	DFI	%M	DY	L*	a*	b*	pH24
Te	0.70	0.12	0.00	0.60	0.64	-0.07	0.54	0.43	-0.51	-0.54	-0.07	0.44	0.34	-0.07
Es		0.23	0.04	0.87	0.51	0.16	0.45	0.43	-0.44	-0.38	-0.03	0.4	0.26	-0.1
Pr			0.44	0.34	0.15	0.23	0.36	0.47	-0.10	-0.13	-0.05	0.09	0.13	0.07
Co				0.08	-0.08	0.00	0.08	0.11	-0.09	0.06	0.17	-0.19	-0.02	-0.12
An					0.45	0.09	0.17	0.19	-0.34	-0.39	-0.16	0.31	0.09	-0.05
Sk						-0.02	0.28	0.23	-0.28	-0.48	0.03	-0.06	-0.02	0.01

[1] Te: testosterone; Pr:progesterone; Co: cortisol; An : androstenone; Sk ; skatole; ADG : average daily gain; FCR : feed conversion ratio; DFI: daily feed intake; %M: carcass leanness; DY: dressing yield

Discussion

Heritabilities. The estimated heritability for androstenone is in the upper range of previously published values (Larzul, 2021). The heritability value of skatole content was expected to be lower, according to results published in the literature (Larzul, 2021). It is recognised that skatole is more subject to environmental effects than androstenone. The heritability of estradiol is higher than those estimated in a population of Landrace (h^2 = 0.65) in Norway (Grindflek et al., 2011) and much higher than the values estimated in German Landrace (h^2 = 0.09) (Brinke et al., 2021). The result can probably be explained by a stricter standardisation of the sampling and/or by the higher age and weight of the animals in the present study. The lower heritability of testosterone compared to estradiol (Grindflek et al., 2011; Dugué et al., 2020), confirmed by this study, is explained by a production of testosterone that is pulsatile and more sensitive to changes in the environment and stress. Few published results exist for the heritability of plasma cortisol in pigs In Landrace, at the end of fattening, Kadowaki et al. (2012) estimated a plasma cortisol heritability value of 0.2 and Brinke et al. (2021) of 0.11. The differences with the present study could be explained by breed or age at sampling. Knowing that cortisol heritability seems higher in a stressful situation (Larzul et al., 2015), it is possible that the measured level does not reflect the basal level, as at the time of blood sampling, the animals were already isolated, for their departure to the slaughterhouse.

Genetic correlations. As expected, the genetic correlations between testosterone, estradiol and androstenone are high and in agreement with the published values (Larzul, 2021). Grindflek et al., 2011 estimated much higher correlation values between these traits (from 0.8 to 0.95) in Landrace populations than those of the present study. In contrast, Brinke et al. (2021) published correlations of the same magnitude (from 0.49 to 0.89). These high correlations reflect the common metabolic pathways for these steroids (Robic et al., 2014). The genetic correlations between, on the one hand, the steroids produced by the testes (androstenone, estradiol and testosterone) and, on the other hand, the steroids produced mainly by the adrenal glands (progesterone and cortisol) are weak (from zero to 0.34). Considering Brinke et al. (2021) and present results, it can be assumed that the steroid activity of the adrenal glands and testes are poorly genetically related.

Growth rate is not genetically related to any of the measurements except with progesterone (r_g= 0.23). FCR and DFI are positively correlated not only with testicular hormones but also

with progesterone, suggesting an overall genetic relationship with steroid metabolism. In contrast, %M is negatively correlated with testicular hormones, and more particularly with testosterone. This result is contrary to expectations, given that testosterone is known to have an anabolic effect on muscle. However, it should be considered that the animals were in the process of puberty and low levels of testosterone and estradiol indicate an early stage of sexual maturity for individuals just starting to deposit fat. The negative genetic correlations between %M and androstenone or skatole are consistent with the fact that the leaner lines are less at risk of developing boar taint (Larzul, 2021). The negative and moderate genetic correlation between yield and skatole might be related to viscera development. The pH measured 24 hours post mortem is not genetically linked to steroid hormones and odorant compounds as already shown by Dugué et al. (2020) in Pietrain. As for the colour parameters, they are moderately correlated with estradiol and testosterone (around 0.3) as well as with androstenone for the red index ($r_g = 0.31$). The links between steroids and meat quality could result from the pubertal stage of development of the animals. In general, less mature stages are associated with lighter and less red meat, thus individuals more advanced in their pubertal development would have darker meat with a higher red index.

The estimation of the genetic parameters on boar taint related traits in one of the main French maternal lines shows that overall selection against boar taint will have indirect responses similar to those of the sire lines. However, in these maternal lines, it is also imperative to estimate the genetic relationships between boar taint risk (in males) and reproductive traits (in related females).

References

Batorek N., Škrlep M., Prunier A., Louveau I., Noblet J. *et al.* (2012) J. Anim. Sci. 90:4593-4603.

Brinke I., Grosse-Brinkhaus C., Roth K., Pröll-Cornelissen M.J., Klein S. *et al.* (2021) Animals 11:231.

Dugué C., Prunier A., Mercat M.J., Monziols M., Blanchet B. *et al.* (2020). Animal 1:1333–1341.

Grindflek E., Meuwissen T.H.E., Aasmundstad T., Hamland H., Hansen M. H. S. *et al.* (2011) J. Anim. Sci. 89:680-692.

Kadowaki H., Suzuki E., Kojima-Shibata C., Suzuki K., Okamura T., *et al.* (2012) Livest. Sci. 147:20–26.

Larzul C., Terenina E., Foury A., Billon Y., Louveau I., *et al.* (2015) Animal 9:1929-1934.

Larzul C. (2021) Animals, 11:699.

Neumaier A. Groeneveld E. (1998) Genet. Sel. Evol. 30:3-26.

Robic A., Faraut T., Prunier A. (2014) J. Steroid Biochem. Mol. Biol. 140:44-55.