Genetics of tail-biting receipt in gilts from the Tai Zumu line

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Summary

Tail-biting (TB) receipt was recorded at the end of the fattening period on 33,266 gilts of the Tai Zumu population, that were raised in groups of 6 to 20 females. This study aimed at quantifying the contribution of social genetic effects to TB receipt, and at assessing the importance of the environment on the genetic expression of this behaviour (GxE). Models for TB receipt included the fixed effects of number of group mates, (herd)-year-month, and the random effects of group, litter, and direct and social additive genetic effects. The model was applied to the complete gilt population and separately to 2 sub-populations, corresponding to 2 of the 3 nucleus herds raising that line, where TB receipt frequency differed and was high enough (>5%). TB receipt was analysed as a linear trait, following a normal distribution with the restricted likelihood methodology applied to an animal model. Social genetic effects contributed 81% to 93% of total heritable variance, which equalled 40 to 80% of phenotypic variation. The variance components varied between herds. The analysis of sire by environment interactions indicated re-ranking of sires between the 2 nucleus herds, according to both their direct and total breeding values.

Keywords: social genetic effects, tail-biting receipt, gilt, sire-environment interaction

Introduction

Pig behaviour refers to complex traits which expression depends on physical and social environments. Tail-biting (TB) is a damaging behaviour that is highly detrimental to animal welfare, resulting in stress, pain, and removal of strongly attacked pigs. Genetic studies of TB are scarce (Breuer et al., 2005) because the frequency of TB is low in pig populations - except outbreaks - and in addition can be under recorded. Bitten tails are more accessible records than the TB activity itself. TB receipt information refers to the receivers of tail bites. Between-breed variation exists for this trait with, for instance, Yorkshire pigs being tail-bitten more often than Landrace pigs (Sinisalo et al., 2012).

In the fattening period, group structure and social relationships might influence the emergence of a TB attack. Social effect of a pig on the phenotypes of its social partners may have a genetic component (Griffing 1967; Moore et al., 1997), known as an Indirect Genetic Effect (IGE). IGEs refer to the effects of an individual's genes on the trait values of other individuals. We hypothesized that TB receipt is affected by IGEs, so that pigs would participate to the emergence of tail bites in their groupmates. Moreover, estimates for the social genetic effect are sensitive to environmental conditions (e.g., Bijma, 2011, Canario et al., 2017). The response to selection against TB receipt might be quite different if pen size, group size, as well as food availability, varied between herds. Our objectives were to estimate the genetic parameters for TB receipt with social genetic effects, and to evaluate sire by environment interactions (GxE) for this trait in differing nucleus herds.

Material and methods

Animals and data

The Tai Zumu line is a composite line made from the combination of Meishan and Large White genetics. Animals are raised in 3 nursing-fattening nucleus herds located in diverse regions of France. Connectedness was ensured by use of common AI boars across herds (among 1010 sires with progeny records, >200 enabled to connect the differing herds 2 by 2). Piglets are half tail-docked in the first 24h after birth, experience mixing after weaning, and then pigs entering the fattening unit are not mixed again (Herds 1 and 3) or split into 2 groups (Herd 2). During the fattening period, average group size of the female population was 12.3 (SD 3.6). The 3 herds differed in average group size $\bar{n}$: 8.5 (SD 1.0), 12.7 (SD 1.9) and 14.7 (SD 3.9) animals/pen in Herds 1, 2 and 3 (p<0.0001). Herds also differed in the number of litters of origin included in a group: 5.3 (SD 1.1), 6.8 (SD 1.8) and 6.1 (SD 1.4) in Herds 1, 2 and 3 (p<0.0001). Such contrasts remained after adjustment for group size, with mean values of 5.9, 6.4 and 5.4 in Herds 1 to 3 (p<0.0001). Pigs were raised in single sex-groups and fed *ad libitum* from one single trough (Herds 1 and 2) or a dry feeder (Herd 3). The stocking density was 0.78, 0.82 and 0.85 pigs/m² in Herds 1 to 3. The TB receipt information was summed up as a yes/no trait, from tail bite(s) records realized by a single observer for all 3 herds, at time of control when pigs reach 100kg on average. Data used in the current study were collected between 2006 and 2017 from 2970 fattening groups. The number of litters of origin to form a group varied between 1 and 12, with total group size ranging between 6 and 20. The TB receipt involved 852 groups (31% of groups), in which on average 2.8 (SD 2.4 range 1-17) pigs were injured. The removal of injured pigs before the end of the fattening period was infrequent, so severity of tail bites was not high.

Statistical analyses

Data were edited with the SAS software to create group and batch variates and groupmates identities. In the complete data base, 7.9% of females that were measured became mothers and 2.9% of females with tail injured became mothers. TB receipt was analysed as a linear trait with the REML procedure of the ASReml software (Gilmour et al., 2015). The pedigree included information from animals recorded over the 11 years plus was traced back 2 generations more.

Social models

With social interactions, the trait value of a pig may be affected by genes in other pigs. To investigate the magnitude of IGEs on TB receipt, we analysed the presence of tail bite(s) as a normally distributed trait, although the risk of bias exists especially when the frequencies between the two classes of the binary trait are highly unbalanced (Meijering and Gianola, 1985). The model included the fixed effects of number of group mates (15 levels), the combination of herd, year and month as a factor, and the random effects of the group identity and the litter of birth. The goodness of fit was used to compare nested models following a chi-square statistics. The selection of random effects was applied to 3 data bases including the complete population and 2 sub-populations originating from 2 of the 3 farms where the incidence of tail-biting was substantial (>5%). In the model for the 2 sub-populations, the combination of herd, year and month was replaced by a year and month combination. In all analyses, the selected model was as follows: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_D \mathbf{a}_D + \mathbf{Z}_S \mathbf{a}_S + \mathbf{Vg} + \mathbf{Wl} + \mathbf{e}$ where $\mathbf{y}$ is a vector of observations on the TB receipt; $\mathbf{X}$, $\mathbf{V}$ and $\mathbf{W}$ are known incidence matrices; $\mathbf{b}$ is a vector for fixed effects; $\mathbf{a}_D$ is a vector of direct additive genetic effects of the focal pig, and $\mathbf{a}_S$ is a vector of IGEs, i.e., social genetic effects of the groupmates of the focal pig. The model accounted for a covariance between direct and indirect genetic effects, using the variance structure $\begin{bmatrix} \mathbf{a}_D \\ \mathbf{a}_S \end{bmatrix} \sim MVN \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_{A_D}^2 & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma_{A_S}^2 \end{bmatrix} \otimes \mathbf{A} \right)$ where $\mathbf{A}$ denotes the matrix of additive genetic relationships with $\sigma_{A_D}^2$ the direct additive genetic variance, $\sigma_{A_S}^2$ the variance of an IGE expressed on a single groupmate and $\sigma_{A_{DS}}$ the co-variance between direct and indirect genetic effects. Next, $\mathbf{g}$ is a vector of random group effects, with $\mathbf{g} \sim N(0, \mathbf{I}\sigma_g^2)$; $\mathbf{l}$ is a vector of random litter effects, with $\mathbf{l} \sim N(0, \mathbf{I}\sigma_l^2)$; and $\mathbf{e}$ is a vector of residuals, with $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$. $\mathbf{Z}_D$ and $\mathbf{Z}_S$ are known incidence matrices for the direct and social genetic effects, linking respectively own identity and group mates to the record of a pig. The phenotypic variance was calculated as $\sigma_P^2 = \sigma_{A_D}^2 + \sigma_g^2 + \sigma_l^2 + (\bar{n}-1)\sigma_{A_S}^2 + \sigma_e^2$ where $\bar{n}$ denotes the average group size of the population. The total genetic variance equals $\sigma_{TBV}^2 = \sigma_{A_D}^2 + 2(\bar{n}-1)\sigma_{A_{DS}} + (\bar{n}-1)^2\sigma_{A_S}^2$ (Bijma et al., 2007). The total heritable variance was expressed as $T^2 = \sigma_{TBV}^2 / \sigma_P^2$, and the comparison between T^2 and h_d^2, the classic heritability, reveals the impact of social interactions on the heritable variation that determines

the potential of the population to respond to selection.

Measurement of GxE

To get an insight in the magnitude of GxE, we compared outputs from the social genetic model described above, applied within 2 sub-populations. The classic approach of carrying out a bi-variate genetic analysis, where each trait is defined by a sub-population, did not reach convergence. Breeding values for TB receipt were estimated from a_D that refers to random direct genetic effects related to the direct estimated breeding value denoted **DBV**, and a_S that corresponds to the summed social genetic effects applied from 1 pig from a group of n individuals on its group mates and is related to the social breeding value denoted **SBV**. The total heritable contribution of genes of a single individual *i* in environment *j* on the mean trait value, i.e., the total breeding value ($\textbf{TBV}_{ij}$) was calculated as: $\text{TBV}_{ij} = \text{DBV}_{ij} + (n\text{-}1)\,\text{SBV}_{ij}$ with *n* the group size of the focal pig. Spearman rank correlations between DBVs, SBVs and TBVs for the 59 boars which were widely used as sires across the 3 herds, i.e., with ≥ 20 daughters measured for TB receipt in each herd, were calculated.

Results and discussion

Social effects on damaging behaviour may differ between sexes. The general suggestion is that female pigs are more likely to tail bite their conspecifics than male pigs, and this results in more tail damage (Zonderland et al., 2010). The frequency of TB receipt in Tai Zumu males was very low (0.06% in Herd A, 1.3% in Herd B and 3.8% in Herd C). We focused our study on female groups, where the frequency of TB receipt varied from 2.8% (Herd 1) to 10.8% with significant contrasts between herds (P<0.0001). The estimates of variance components of TB receipt obtained from use of the direct-social model are given in Table 1.

Table 1. Variance components estimates (s.e.) for tail-biting receipt in Tai Zumu gilts from different herds and the all population.

Herd	2	3	All population
N	12375	11856	33266
TB receipt (%)	6.6	10.8	7.1
$\sigma^2_{A_D}$	0.322 (0.066)[1]	0.759 (0.157)	0.353 (0.049)
$\sigma^2_{A_S}$	0.012 (0.0038)	0.019 (0.005)	0.032 (0.0037)
σ^2_P	5.753 (0.087)	8.94 (0.157)	5.932 (0.055)
σ^2_{TBV}	2.300 (0.610)	3.966 (0.944)	4.749 (0.529)
h^2_d	0.06 (0.01)	0.08 (0.02)	0.06 (0.01)
$\hat{T}^2$	0.40 (0.11)	0.44 (0.11)	0.80 (0.09)
$r_{A_{DS}}$	0.19 (0.19)	-0.13 (0.18)	0.11 (0.10)
σ^2_g	0.717 (0.077)	1.323 (0.143)	0.519 (0.049)
σ^2_l	0.103 (0.037)	0.467 (0.076)	0.235 (0.027)

[1] Estimated variances should be multiplied with a 10^{-2} factor.

The direct-social model fitted the data significantly better than the direct model in the 3 (sub-)populations (P<0.0001). The estimates for $\sigma^2_{A_D}$, σ^2_P, and σ^2_l were very close to those obtained from use of a direct model. The estimate for σ^2_ε decreased by half in the all population when adding social components. The phenotypic variance varied between herds, being one and a half times higher in Herd 3 than in Herd 2. Both direct genetic variances and group variances were heterogeneous between herds. Direct heritability for TB receipt was low (0.06 to 0.08) in the 2 herds under study and estimated at 0.06 in the whole population. Group effects were moderate, and accounted for 8.7 to 14.5% of phenotypic variation. The litter effects explained a lower part of variation in Herd 2 than in Herd 3, due to the mixing of pigs from numerous litters of origin to create a group. Litter effects explained only 1.8% and 5.2% of phenotypic variation in Herds 2 and 3 respectively, that let us presume of low early-life effects on TB receipt (Canario et al., 2017).

The total heritable variance increased markedly with average group size, from Herd 2 to Herd 3. The contribution of social effects to heritable variation in TB receipt stands in the difference between $\sigma^2_{A_D}$ and σ^2_{TBV}. Social effects contributed highly to heritable variation when the population was considered as a whole (93%), which contrasts with results obtained for growth rate (e.g., 44% in Canario et al., 2017). The contribution of social effects was high in Herds 2 and 3 (86% and 81%, respectively). Total heritable variation was moderate in the 2 herds under study. The genetic correlation between direct and social effects was null when considering the all population as well as Herds 2 and 3. Social structures might not differ between the two herds, with neutral associations among gilts meaning that gilts with a higher genetic predisposal for receiving tail bites do not increased the probability of other gilts in the group to be tail bitten.

The rank correlations of boars's direct, social and total breeding values are assumed to be consistent with the true genetic correlations (McLaren et al., 1985). A strong re-ranking of sires in the two herds was observed.

Table 2. Means and standard deviations (SD) of breeding values and Spearman rank correlations between DBV, SBV and TBV for the 59 more used sires across herds.

	Herd 2		Herd 3		Herds 2 vs 3	
	Mean	SD	Mean	SD	Rank correlation[1]	p-value H0: r=0
DBV	0.0023	0.0285	-0.0128	0.0490	0.09 (-0.17 / 0.34)	0.49
SBV	-0.0007	0.0045	0.0030	0.0069	0.12 (-0.14 / 0.36)	0.37
TBV	-0.0038	0.0617	0.0163	0.0804	0.13 (-0.13 / 0.38)	0.32

[1] Estimated correlations between breeding values for Herd 2 in comparison to Herd 3 (2vs3)
95% confidence intervals are given between brackets.

Correlations between Herds 2 and 3 were not different from zero, indicative of strong interactions with the herd environment (Table 2). Differences in average group size and feeding might be involved in the detection of sire by environment interactions. According to DBVs, the more highly used sires ranked differently between Herds 2 and 3. The correlations were far lower than those estimated by Wallenbeck et al (2009) in the comparison of growth rate and backfat thickness between conventional and organic herds (r=0.48). High sire by

environment interactions are not surprising for a trait that is not under control by selective breeding. It is important to account for GxE in order to increase response to selection. It should be advised to select sires that are less sensitive to environmental conditions when implementing a selection against gilts that suffer from this aberrant behaviour, i.e., that have a genetic predisposal to let others bite their tail. When considering TBV, the correlation was also zero between Herds 2 and 3. Selection based on TBV rather than DBV would not attenuate the discrepancies between the two herds in the ranking of best sires. Considering only the 19 sires with stable DBVs across the two herds, several suffered from large re-ranking according to TBVs (Appendix 1).

Estimating the influence of IGEs on TB receipt was partly a challenge, given the substantial but low incidence of the trait in these populations. Estimates rely much on group composition, with only 29% of groups being informative, i.e., with ≥1 female with tail bitten. Another problem depended upon the extreme categories and it would be limited by use of a sire model. Some bias may result from the use of standard linear models to analyse a binary trait, but linear models are known to be robust to strong departures from normality assumptions. This study provides first estimates of tail-biting receipt genetic parameters, with account for significant social genetic effects.

Conclusion

Selection against Tai Zumu gilts that let other gilts bite their tail is feasible, and would gain from including social genetic effects as regards to response to selection. With strong GxE identified on TB receipt that resulted in important re-ranking of sires - according to breeding values - in the differing environments, we conclude that TB receipt is influenced partly by different genes in the 2 herds. Selecting for boars that maintain a low genetic merit for their gilts to be tail bitten across varying environments is relevant. Selecting for TBV instead of DBV would either decrease or accentuate the contrast in ranking of AI sires across environments. Further research will be carried out to analyse the impact of the environment on the genetics of this damaging behaviour. At the genetic level, tail biting activity is unfavorably correlated with growth rate and leanness (Breuer et al., 2005). Genetic relationships of TB receipt with performance traits will be investigated in future studies of the Tai Zumu line.

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Appendix 1
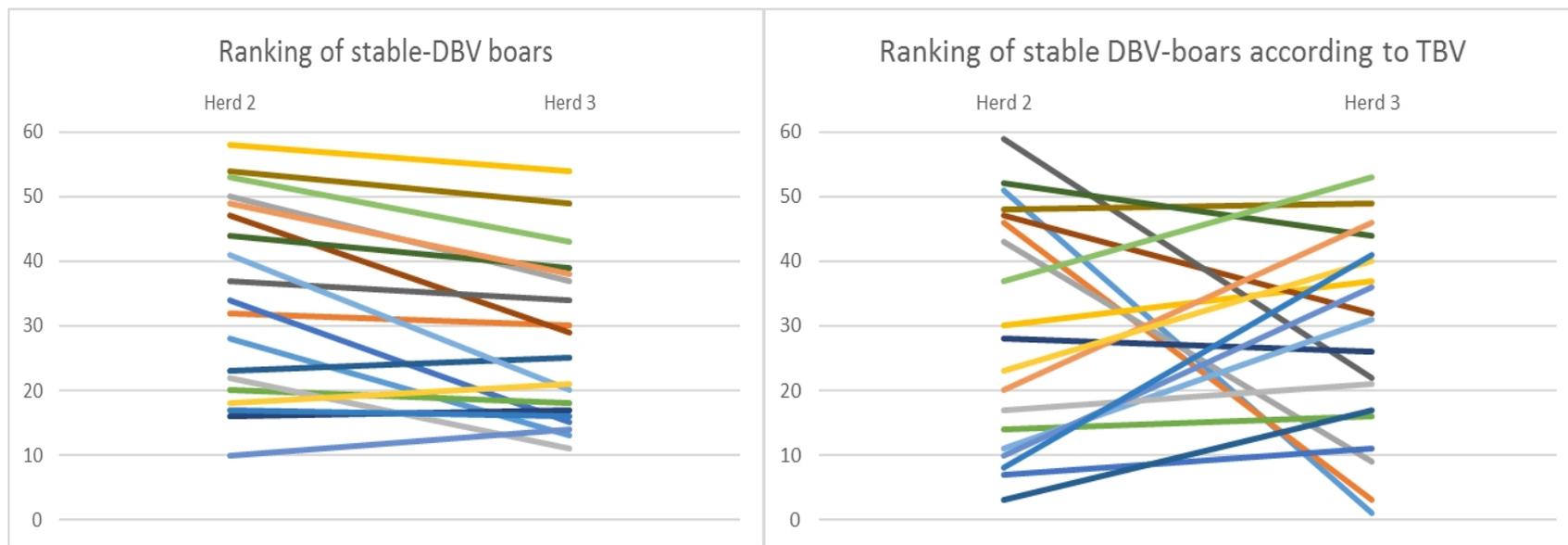
Among the 59 sires, 19 sires with DBVs considered as stable across the 2 herds under study (Herd 2 and Herd 3) were identified (left figure) and ranked according to TBVs (right figure)