Journal of Agricultural Science (2016), **154**, 732–741.
doi:10.1017/S0021859616000010

ANIMAL RESEARCH PAPER

Estimation of genetic parameters for agonistic behaviour of pigs at different ages

K. SCHEFFLER[1]*, E. STAMER[2], I. TRAULSEN[1] AND J. KRIETER[1]

[1] *Institute of Animal Breeding and Husbandry, Christian-Albrecht-University, Olshausenstr. 40, 24098 Kiel, Germany*
[2] *TiDa Tier und Daten GmbH, Bosseer Straße 4c, 24259 Westensee/Brux, Germany*

(*Received 11 November 2013; revised 1 September 2015; accepted 5 January 2016; first published online 4 March 2016*)

SUMMARY

The mixing of pigs unacquainted with each other in commercial pig production is a standard procedure which leads to agonistic interactions with a wide range of individual pig behaviour. Hence, the aims of the present study were to assess the heritabilities of agonistic behaviour and to estimate correlations between three different age groups (weaned pigs $n = 1111$, growing pigs $n = 446$ and breeding gilts $n = 279$). The behavioural observation analysis included a period of 17 h directly after mixing as weaned pigs, growing pigs and breeding gilts (220 days of age) whereby the following agonistic traits were observed: number of fights (NF), duration of fights (DF), initiated fights (IF), received fights (RF), fights won (FW) and fights lost (FL). The behaviour of the weaned and growing pigs was significantly influenced by cross-fostering, their weight at mixing and litter attributes. Cross-fostered animals showed fewer agonistic interactions as weaned pigs and as growing pigs than non-cross-fostered animals. The influence of weight revealed that heavier pigs had a higher NF score at weaning and as growing pigs. The random litter effect explained up to 0·08 of the total variance in weaned and 0·04 in growing pigs, whereby this could partly be explained by litter size. Pigs from larger litters tended to have more agonistic interactions. The heritabilities of the recorded traits were at a low to medium level but similar between the age groups. There were high correlations between NF and all other traits in weaned pigs. The trait IF showed that the more fights a pig initiated, the more it won. This was also found for growing pigs and breeding gilts. The relationships between the age groups provided no uniform trend. The phenotypic correlations were low and the genetic correlations varied widely, partly due to the small sample size.

INTRODUCTION

The importance of behaviour in the breeding and husbandry of pigs is becoming more important, especially regarding animal welfare aspects. Social groups in modern pig production are not stable; for example, the mixing of unacquainted pigs after weaning, at the beginning of the growing period or in breeding herds is a common practice (Ismayilova *et al*. 2013). In order to establish a stable hierarchy and to prevent permanent stress within the group, fights take place between the animals. The interaction of pigs using aggressive and submissive behaviour is called agonistic behaviour. Less aggressive animals do not negatively influence other pigs, for example, due to stress or injuries (Tuchscherer & Manteuffel 2000). Hence, excessive aggression, especially towards low-ranking pigs, can influence welfare, health and weight gain, which are important factors in pig production (Tan *et al*. 1991; Stookey & Gonyou 1994). Therefore, one possible way to reduce aggression and increase animal welfare is the breeding of calm and less aggressive pigs (Erhard *et al*. 1997; D'Eath *et al*. 2009). Presently, some breeding organizations include traits regarding behaviour and aggression as subordinated goals in their breeding programmes. In order to use traits concerning agonistic interactions it is important to know their heritability, but only a few estimates have been published on this so far (Løvendahl *et al*. 2005; Turner *et al*. 2008, 2009; Stukenborg *et al*. 2012). For growing pigs, a wide range of heritability for agonistic behaviour has been estimated (Turner *et al*. 2008, 2009). According to Stukenborg *et al*. (2012), heritabilities for

* To whom all correspondence should be addressed. Email: kscheffler@tierzucht.uni-kiel.de

growing pigs and breeding gilts (242 days of age) are higher than those for weaned pigs, possibly as a result of confusion between playing and fighting in young pigs (Chaloupková *et al*. 2008; Silerova *et al*. 2010). Aggression is a more stable temperament trait in older pigs. Even so, fighting in weaned pigs, growing pigs and in breeding gilts is motivated mainly by the attempt to establish a rank order. Agonistic interactions have been recorded by behavioural observations in several studies. In contrast, ontogenetic analysis of the aggressive and submissive behaviour has been less well-documented. Comparisons of agonistic interaction at different stages of life show that stronger relationships exist between growing pigs and breeding gilts than between weaned and growing pigs or between weaned pigs and breeding gilts (Stukenborg *et al*. 2012). However, Stukenborg *et al*. (2012) worked with focus animals (i.e. only a few pigs in the pen were marked), meaning that not every agonistic interaction was recorded.

The aim of the present study was to examine the systematic effects on different traits related to agonistic interactions in weaned pigs, growing pigs and breeding gilts. Furthermore, heritabilities of six behavioural traits and correlations between these traits in three different age groups were estimated to describe the pig's ontogenetic development of aggression towards conspecifics. The present results will be compared in further investigations with results of behavioural tests for the prediction of pig behaviour at early ages using standardized test situations.

MATERIALS AND METHODS

Animals and housing

Data were recorded from December 2010 to August 2012 on the research farm 'Hohenschulen' of the Institute of Animal Breeding and Husbandry of the University of Kiel (Germany). The pigs were purebred and crossbred animals of the breeds German Landrace (DL) and German Edelschwein (DE). The piglets from 139 litters (16 sows per batch) were kept in farrowing pens for 26 days postpartum (suckling period). The building consisted of four rooms each with eight pens. These conventional farrowing pens measured $2{\cdot}2 \times 1{\cdot}7$ m^2 and had a tiled and metal base floor with no substrate. The lactating sows received a commercial lactating feed in accordance with the German norm (GfE 2006). Water was accessible through nipple drinkers. A piglet feeder was open to the piglets from the first week after farrowing. Each live born piglet was marked and weighed individually (average weight $1{\cdot}54 \pm 0{\cdot}188$ kg at the first day of age. Within the first 3 days, 0·175 of the total number of piglets were cross-fostered to standardize the litter size (litter size = number of live born piglets). The cross-fostered piglets were the heaviest piglets of the litter. All male piglets were castrated.

At weaning, the pigs ($n = 1111$) were weighed individually (average weight $8{\cdot}8 \pm 0{\cdot}68$ kg) and then housed in flatdecks. There were four rooms with ten pens each. The dimension of one pen was $2{\cdot}05 \times 1{\cdot}36$ m^2 and had a concrete and metal base floor with no substrate. Two nipple drinkers were available in each pen for *ad-lib* water use. The pigs were fed *ad libitum* with solid pelleted feed in conformity with the German norm (GfE 2006). The room temperature was approximately 24 °C. The pigs were re-mixed and sorted by the smallest level of familiarity and by nearly equal weight. Eight to ten pigs were housed in one pen and no pig knew another pig from the farrowing pens. The pigs stayed in the flatdecks for 6 weeks (on average 44 days).

After 6 weeks in the flatdeck, the pigs ($n = 446$) were re-mixed and re-housed in the growing building in groups of 20–25 animals. The pens had a size of $3{\cdot}25 \times 2{\cdot}40$ m^2 with a half-slatted and solid floor. Nipple drinkers for *ad-lib* water use were accessible. The growing pigs were fed by a wet feeder with a commercial diet (GfE 2006). The temperature was 22 °C. The pigs were sorted by the smallest level of familiarity and by nearly equal body size. In the pens, a maximum of two pen mates already knew each other from the time spent in the flatdeck pens.

At approximately 220 days, the breeding gilts ($n = 279$) were re-mixed and housed in a pen in the breeding area (gilt pen) in groups of 17–28 breeding gilts.

The pen had a dimension of $7{\cdot}2 \times 5{\cdot}4$ m^2 and a half-slatted and solid floor. The breeding gilts were fed according to standards of the GfE (2006). Water was accessible through nipple drinkers. All breeding gilts were sorted by the smallest level of familiarity; hence a maximum of five breeding gilts knew each other from the growing pens.

Behavioural observations

The video observations started at approximately 12:00 h immediately after rehousing at each stage and recorded the pigs' behaviour for 4 days. Stukenborg *et al*. (2011) stated that there was a decline in agonistic behaviour during the night and

Meese & Ewbank (1973) showed that fighting behaviour decreased significantly after 2 days of observation. Therefore, the video recording was interrupted during the night (from 18:00 to 07:00 h). Due to the high number of animals in the study, the period used for the analysis was limited to 17 h (day of housing: approximately 12:00–18:00 h; 2nd day: 07:00–18:00 h). The HeitelPlayer software (Xtralis Headquarter D-A-CH, HeiTel Digital Video GmbH, Kiel, Germany) was used for video analysis of the agonistic interactions. All pigs in a pen were marked individually on their backs and could be observed in the whole pen. Data from 1111 weaned pigs, 446 growing pigs and 279 breeding gilts were used in the statistical analysis.

The start and end of a fight, the initiator and receiver, and the winner and loser of an agonistic interaction were recorded for all marked pigs in the flatdecks, growing building and gilt pen. If the aggressor/receiver or the winner/loser was not clear, the fights were recorded with unclear starter/finisher. Six traits were obtained: total number of fights (NF), duration of fights (DF), number of initiated fights (IF), number of received fights (RF), number of fights won (FW) and the number of fights lost (FL). A fight was defined as a physical contact longer than 1 s with aggressive behaviour initiated by one pig towards another and ended in the submissive behaviour of an involved pig, i.e. the loser of the fight (Tuchscherer *et al*. 1998; Langbein & Puppe 2004). 'Head-to-head knocks', 'head-to-body knocks', 'parallel/inverse parallel pressings', 'bites' or 'physical displacements' were recorded as agonistic behaviour (Puppe 1998; Stukenborg *et al*. 2012; Ismayilova *et al*. 2013). Submissive animals were defined as those which showed typically submissive behaviour, i.e. they stopped fighting, turned away, were displaced from a location or tried to flee (Tuchscherer *et al*. 1998; Langbein & Puppe 2004; Stukenborg *et al*. 2012). The video observations of the weaned pigs in the flatdecks were carried out by three different observers, who observed different animals of all batches. They had been trained using video test sequences at the beginning of the video analysis. The definition and identification of the agonistic behaviour was tested with an unknown video sequence. The inter-observer agreement was >0·90. The videos of the growing pigs and breeding gilts were analysed by one person only.

Statistical analysis

The statistical analyses were performed using the SAS® statistical software package (SAS 2008) and the variance components were estimated using the software VCE (Kovac & Groeneveld 2007). All traits of the original data had a non-normal distribution. Therefore, the descriptive statistics used the medians of the data. Further calculations were performed with log-transformed data ($Y = \log_e$ (1 + observation value)) in order to reduce the skewness. After transformation, the skewness of the weaned pigs ranged from −0·77 to −0·1, for the growing pigs from 0·23 to 1·08 and for the breeding gilts from −0·46 to 0·42 between the traits. The kurtosis of the traits had a range of −0·63 to 0·76 for weaned pigs, of −0·79 to 1·03 for growing pigs and of −0·05 to −0·74 for the breeding gilts. Therefore, after log-transformation, the agonistic behavioural traits were approximately normally distributed, as also confirmed by visual inspection of the residual plots.

Analysis of the relevant systematic effects was performed using the procedure MIXED in SAS (SAS 2008). The Maximum Likelihood Estimation was used to test different models and fixed effects were added stepwise in the models (ignoring all random effects). Evaluation of goodness of fit to the different models was carried out using Akaike information criterion (AIC) and Bayesian information criterion (BIC) (Schwarz 1978; Hurvich & Tsai 1989). The smaller the AIC and BIC the better was the fit of the model.

The heritabilities of the traits and the genetic and phenotypic correlations between the traits in the different age groups were estimated by an animal model using the software program VCE-6 (Kovac & Groeneveld 2007). Before using VCE-6, the data were prepared with the program PEST (Groeneveld 1990). The pedigree contained two previous generations (parents and grandparents) and sows were mated to one of 60 sires. On average, each sire had 23 offspring and each sow 13 offspring. Sires produced both pure- and crossbred progeny (breeds: Large White 136, German Landrace 12, crossbreeds 1121). The final models for the different traits were the same within one age group (Model I: weaned pigs; Model II: growing pigs; Model III: breeding gilts).

$$\text{Model I } Y_{ijklmno} = \mu + B_i + OB_j + PEN_k + CF_l + b \times W_{ijklmno} + lit_m + ani_n + e_{ijklmno}$$

$$\text{Model II } Y_{ilmno} = \mu + B_i + CF_l + b \times W_{jlmno} + lit_m + ani_n + e_{ilmno}$$

$$\text{Model III } Y_{imno} = \mu + B_i + b \times W_{imno} + lit_m + ani_n + e_{imno}$$

https://doi.org/10.1017/S0021859616000010 Published online by Cambridge University Press

where $Y_{ijklmno}$ = observations of traits NF, DF, IF, RF, FW, FL of weaned pigs; Y_{ilmno} = observation of traits NF, DF, IF, RF, FW, FL of growing pigs and Y_{imno} = observation of traits NF, DF, IF, RF, FW, FL of breeding gilts; μ = overall mean; B_i = fixed effect of batch (i = 1–10); OB_j = fixed effect of observer (j = 1, 2, 3); PEN_k = fixed effect of pen (k = 1–40); CF_l = fixed effect of cross-fostering (l = 1, 2); $b \times W_{ijklmno}$ = linear regression on weight at rehousing; lit_m = random effect of litter (m = 1–139); ani_n = random additive genetic effect of the nth animal (n = 1–1273). Fixed effects not reducing the fitting parameters AIC and BIC were removed (e.g. gender, parity of the sow, number of pen mates, pen and breed type).

RESULTS

Behavioural performance

Descriptive statistics of the agonistic behaviour in the three age groups are presented in Table 1. Weaned pigs had the highest and breeding gilts the lowest number of fights (NF). The weaned pigs fought for a total of 387 seconds, the growing pigs for 279 s and breeding gilts for 174 s. Considering all traits, it was shown that the older the pigs were, the fewer agonistic interactions could be observed.

Fixed and random effects

With the exception of DF, the observer significantly influenced all the traits of the weaned pigs ($P<0{\cdot}01$). Testing linear contrasts of the three observers, it could be seen that one observer had significantly different results for the agonistic interactions from the other two ($P<0{\cdot}05$). However, results were unchanged when data from the outlier observer were removed.

Cross-fostering influenced the agonistic interactions of the weaned pigs and the growing pigs. For example, back-transformation of LS Means for the NF trait showed that in weaned pigs: $NF_{cross\text{-}fostered}$: 13·3 ± 0·05, $NF_{non\text{-}cross\text{-}fostered}$: 15·0 ± 0·03; $P<0{\cdot}05$ as well as in growing pigs: $NF_{cross\text{-}fostered}$: 4·3 ± 0·09, $NF_{non\text{-}cross\text{-}fostered}$: 6·0 ± 0·5; $P<0{\cdot}05$. The same effect was observed for the other traits. Pigs which had not been raised by their own dam showed fewer agonistic interactions and were less aggressive than non-cross-fostered animals. The behaviour of the breeding gilts was no longer influenced by cross-fostering.

Table 1. *Median, minimum and maximum of behavioural traits (number of fights: NF; duration of fights: DF; initiated fights: IF; received fights: RF; fights won: FW; fights lost: FL) for three different age groups*

	Weaned pigs (n = 1111)					Growing pigs (n = 446)					Gilts (n = 279)				
	Median	Min	Max	S.D.	D.F.	Median	Min	Max	S.D.	D.F.	Median	Min	Max	S.D.	D.F.
NF	15	1	116	20	1110	6	0	39	6	445	4	0	32	6	278
DF (s)	387	2	4647	526	1110	279	0	7672	1057	445	174	0	3623	807	278
IF	5	0	68	8	1110	3	0	24	4	445	1	0	28	4	278
RF	6	0	37	8	1110	3	0	18	3	445	1	0	15	3	278
FW	5	0	98	9	1110	2	0	24	4	445	1	0	31	4	278
FL	7	0	52	9	1110	3	0	19	3	445	2	0	17	3	278

S.D., standard deviation; D.F., degrees of freedom; s, seconds.

https://doi.org/10.1017/S0021859616000010 Published online by Cambridge University Press

The weight at rehousing, at weaning or in the growing building influenced the agonistic behaviour of the pigs significantly, with heavier pigs fighting more than lighter pigs. The slopes of the linear regression of weight *v*. NF were 0·06 ± 0·010 (P < 0·05) for the weaned pigs and 0·03 ± 0·010 (P < 0·05) for the growing pigs. The fighting of breeding gilts was not influenced by the weight of the animals.

The estimated variances of the random animal effect (additive genetic effect), random litter effect and the residual effect are shown in Table 2. In weaned pigs, the proportion of the total variance explained by litter effects ranged from 0 to 0·08. In growing pigs, this proportion was lower (0–0·04). The behaviour of breeding gilts was not influenced by the litter effect.

Heritabilities

For weaned pigs, the heritabilities ranged from 0·06 for DF to 0·37 for RF (Table 2). Heritabilities for NF, FW and FL were similar (0·15–0·22). In growing pigs, the heritabilities did not differ substantially between the recorded behavioural traits (0·11–0·18), apart from DF, which was not heritable. The heritabilities for the breeding gilts ranged between 0·01 (FL) and 0·12 (FW). All heritabilities were estimated with high standard errors in all age groups for most traits.

Correlations between behavioural traits within different age groups

The phenotypic and genetic correlations between the behavioural traits are shown in Table 3. Nearly all traits were phenotypically and genetically correlated with NF at all ages except for NF and FL in weaned pigs. Initiated fights were highly correlated with the trait FW and RF was highly correlated with FL and DF. Small correlations were found between the traits IF and RF. There was a negative genetic relationship between FW and FL for the weaned pigs. The correlations for the growing pigs and breeding gilts between the recorded traits were high for almost all traits.

Correlations within behavioural traits between different age groups

Table 4 shows the phenotypic and genetic correlations between the three age groups. The phenotypic correlations between the age groups were low. The coefficients ranged from –0·04 to 0·34 within the different

Table 2. *Heritabilities and variances of the animal effect (δa^2 = additive genetic variance), the litter effect (δli^2 = permanent environmental effect) and residual effect (δe^2) for the behavioural traits (number of fights: NF; duration of fights: DF; initiated fights: IF; received fights: RF; fights won: FW; fights lost: FL) at different ages (Weaned Pigs: NF, DF, FW, FL n = 1111 and IF, RF n = 778; Growing Pigs: n = 446; Gilts: n = 279)*

Trait	δ^2_a			δ^2_{li}			δ^2_e			h^2		
	Weaned Pigs	Growing Pigs	Gilts	Weaned Pigs	Growing Pigs	Gilts	Weaned Pigs	Growing Pigs	Gilts	Weaned Pigs	Growing Pigs	Gilts
NF	0·05	0·12	0·07	0·02	0·00	0·00	0·30	0·52	0·66	0·15 (0·090)*	0·18 (0·080)	0·10 (0·110)
DF	0·06	0·01	0·49	0·07	0·13	0·08	0·74	3·51	5·33	0·06 (0·070)	0·00 (0·100)	0·08 (0·110)
IF	0·07	0·09	0·06	0·07	0·02	0·00	0·63	0·57	0·54	0·09 (0·160)	0·13 (0·190)	0·10 (0·110)
RF	0·14	0·05	0·20	0·00	0·00	0·00	0·24	0·41	0·49	0·37 (0·080)	0·11 (0·070)	0·28 (0·100)
FW	0·15	0·07	0·08	0·04	0·00	0·00	0·80	0·60	0·55	0·15 (0·110)	0·11 (0·080)	0·12 (0·110)
FL	0·11	0·07	0·00	0·00	0·00	0·00	0·38	0·37	0·00	0·22 (0·130)	0·16 (0·0800)	0·00 (0·030)

* Standard errors in brackets.

Table 3. *Genetic (r_p) and phenotypic (r_p) correlation of different age stages between the behavioural traits (number of fights: NF; duration of fights: DF; initiated fights: IF; received fights: RF; fights won: FW; fights lost: FL) within the three stages of life*

	DF		IF		RF		FW		FL	
	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p
Weaned pigs										
NF	0·85 ± 0·170	0·82 ± 0·010	0·79 ± 0·190	0·83 ± 0·010	0·62 ± 0·550	0·68 ± 0·020	0·67 ± 0·210	0·77 ± 0·010	0·25 ± 0·750	0·45 ± 0·020
DF			0·48 ± 0·300	0·68 ± 0·020	0·75 ± 0·380	0·55 ± 0·020	0·60 ± 0·260	0·67 ± 0·020	0·08 ± 0·860	0·29 ± 0·030
IF					0·02 ± 0·570	0·28 ± 0·030	0·87 ± 0·070	0·83 ± 0·010	−0·16 ± 0·540	0·20 ± 0·030
RF							−0·05 ± 0·490	0·33 ± 0·030	0·67 ± 0·310	0·57 ± 0·020
FW									−0·54 ± 0·090	−0·03 ± 0·030
Growing pigs										
NF	0·96 ± 0·070	0·88 ± 0·010	0·98 ± 0·130	0·86 ± 0·010	0·87 ± 0·030	0·81 ± 0·020	0·99 ± 0·010	0·81 ± 0·020	0·96 ± 0·060	0·78 ± 0·020
DF			0·90 ± 0·150	0·73 ± 0·020	0·97 ± 0·080	0·70 ± 0·020	0·97 ± 0·100	0·69 ± 0·020	0·85 ± 0·180	0·66 ± 0·030
IF					0·77 ± 0·250	0·48 ± 0·040	0·98 ± 0·030	0·84 ± 0·010	0·99 ± 0·030	0·56 ± 0·030
RF							0·88 ± 0·170	0·55 ± 0·030	0·71 ± 0·210	0·75 ± 0·020
FW									0·14 ± 0·070	0·37 ± 0·040
Gilts										
NF	0·95 ± 0·04	0·93 ± 0·010	0·97 ± 0·020	0·86 ± 0·020	0·99 ± 0·000	0·88 ± 0·010	0·98 ± 0·020	0·88 ± 0·010	0·99 ± 0·010	0·89 ± 0·010
DF			0·90 ± 0·080	0·77 ± 0·02	0·96 ± 0·050	0·79 ± 0·020	0·90 ± 0·060	0·79 ± 0·020	0·95 ± 0·060	0·80 ± 0·020
IF					0·97 ± 0·030	0·60 ± 0·040	0·99 ± 0·010	0·86 ± 0·020	0·99 ± 0·020	0·72 ± 0·030
RF							0·98 ± 0·030	0·74 ± 0·030	0·99 ± 0·010	0·83 ± 0·020
FW									0·20 ± 0·060	0·64 ± 0·040

Table 4. *Genetic (r_g) and phenotypic (r_p) correlations for the behavioural traits (number of fights: NF; duration of fights: DF; initiated fights: IF; received fights: RF; fights won: FW; fights lost: FL) between different age stages*

	Weaned pigs – growing pigs		Weaned pigs – gilts		Growing pigs – gilts	
	r_g	r_p	r_g	r_p	r_g	r_p
NF	0·38 ± 0·440	0·27 ± 0·040	−0·06 ± 0·850	−0·03 ± 0·060	0·39 ± 0·400	0·24 ± 0·060
DF	−0·99 ± 0·290	0·26 ± 0·040	0·99 ± 0·110	−0·03 ± 0·060	0·99 ± 0·010	0·25 ± 0·060
IF	0·99 ± 0·010	0·34 ± 0·040	0·99 ± 0·010	0·02 ± 0·060	0·99 ± 0·010	0·29 ± 0·050
RF	−0·03 ± 0·540	0·14 ± 0·050	0·40 ± 0·010	−0·07 ± 0·060	0·30 ± 0·960	0·07 ± 0·060
FW	0·99 ± 0·030	0·29 ± 0·0400	0·85 ± 0·970	0·06 ± 0·060	0·45 ± 0·450	0·25 ± 0·060
FL	−0·40 ± 0·410	−0·04 ± 0·050	−0·99 ± 0·010	−0·11 ± 0·060	0·99 ± 0·010	0·15 ± 0·060

traits. The lowest values were found for weaned pigs and breeding gilts, demonstrating that the correlations decreased with increasing age differences between the groups. The genetic correlations between the age groups differed from the phenotypic correlations and varied widely between the traits (r_g = −0·06 to 0·99). Very high genetic correlations were estimated for the traits DF, IF and also for some estimations of the traits FW and FL; lower values were obtained for RF and NF. In case of DF and FL, genetic correlations ranged between 0·99 and −0·99 (e.g. for DF it was −0·99 for weaned pigs and growing pigs but it was 0·99 for the other two age comparisons).

DISCUSSION

Fixed and random effects

Despite intensive training on different video sequences, the observers had a significant influence on the recorded traits of agonistic interactions in weaned pigs. This significant effect of the observer implies the necessity for the definition of agonistic interaction to be absolutely clear for all observers and the inter-observer reliability to be continuously verified during the complete analysis of the videos. Linear contrasts between the three observers showed that one had significantly different results compared with the observations of the others. The influence of the divergent observer on the present results, especially on the heritabilities, was tested by excluding the animals observed by this person (n = 348 animals). The estimated heritabilities without these data did not differ from the presented results.

Pigs raised by their own dam had more agonistic interactions at weaning and rehousing in the growing building and were more aggressive than cross-fostered pigs. This effect has been seldom documented in the literature. D'Eath (2004) stated that the pigs that had been socialized before first mixing with unacquainted pigs consistently showed more aggressive behaviour. These pigs established the rank order faster due to the learning of social behavioural skills at an earlier age (D'Eath 2005). However, the experimental design of allowing the interaction of complete litters before weaning (D'Eath 2004) is different to cross-fostering, although a socializing effect is part of both. The cross-fostered pigs learned their social behaviour very early on, as well as how to react when mixed with unacquainted pigs. Therefore, they did not fight very often to establish a rank order. The non-cross-fostered pigs did not have this experience in the first mixing and thus obtained fewer social skills. This might be one explanation for the cross-fostering effect. Furthermore, it is also possible that the aggressiveness of cross-fostered pigs at weaning was reduced by being repeatedly beaten in fights when introduced to the litter in early life. Experiences in early life and success or failure in aggressive interactions had long-lasting effects on the animals (D'Eath 2004). In commercial pig production, the heaviest animals are used for cross-fostering. The weight at weaning and rehousing in the growing building of the cross-fostered and non-cross-fostered animals was compared in the present study to avoid an effect of the weight of the pigs on the cross-fostering effect. Here, no significant differences in weight were found. The cross-fostering had no influence on the behaviour of the breeding gilts. Another point which should be discussed in further studies on the cross-fostering of pigs is how pigs that have never previously been introduced to foreign pigs react. In the present study, a distinction between these pigs and others was not possible.

In the literature, different results can be found regarding the influence of the weight of the pigs on the agonistic behaviour. Litten *et al.* (2003) and Turner *et al.* (2011) stated that there is an influence of weight on the behaviour of the pigs. Heavier pigs were more active and more dominant in their studies. In contrast, Fels & Hoy (2013) obtained no differences between agonistic interactions in groups sorted into light and heavy pigs. The present results do indeed show an influence of weight, which means that the heavier the pigs were, the more aggressive they were. This was observed in weaned pigs as well as in growing pigs. An explanation might be the ability of the heavier pigs to protect their own rank position from the last group of conspecifics (e.g. in the flatdeck) against the new and unacquainted pigs after remixing (e.g. in the growing building). This would support earlier observations that the previous dominance rank has a prolonged effect on the rank position in later groups (Otten *et al.* 1997; D'Eath 2004). The present results also show that the heavier pigs initiated more fights, which also could be explained by the consciousness of the pigs of their own rank position. The influence of weight decreased with the age of pigs. The variation in weight between the breeding gilts was lower (10%) than between the growing pigs (15%) and weaned pigs (20%), which could explain why weight had no impact on the agonistic interactions in breeding gilts.

The random litter effect explained small parts of the whole variance in weaned and growing pigs. The older the pigs were, the smaller the influence of the litter became and therefore the highest proportions of litter variance were found for the weaned pigs. In contrast, the behaviour of the breeding gilts was not affected by the litter component. The litter effect describes the maternal genetic and maternal environmental effect (Roehe *et al.* 2009). Stukenborg *et al.* (2012) stated that the behaviour of the pigs was influenced by pre-weaning experiences, illustrated by the litter effect. Events before farrowing could also substantially influence the development of the brain and the behaviour of the animals (Champagne & Curley 2005). D'Eath & Lawrence (2004) stated that pigs from larger litters were more aggressive compared with smaller litters. This has also been explained by competition between piglets for a teat, or in general for a limited food resource (Fraser 1975; Fraser & Jones 1975). The influence of the litter effect in the present study was tested to determine whether there were differences due to the litter size and the behaviour of the pigs. It was shown that pigs from larger litters tended to have more agonistic interactions ($P \leqslant 0{\cdot}1$) and therefore, it might explain part of the random litter effect.

Heritabilities

The heritabilities of NF, IF and FW were nearly the same for all age groups but differed for RF and FL across ages. Stukenborg *et al.* (2012) found different heritabilities between the traits and ages. They explained the differences via enhanced playing behaviour of the weaned pigs, which affected the ability to record real fighting in this age group. Hence, the results of the present study contradict expectations that the heritabilities in weaned pigs are (normally) lower than in growing pigs and breeding gilts. One explanation might be offered by Silerova *et al.* (2010), who found that fighting and playing behaviour in weaned pigs could not be separated from each other. In the studies of Turner *et al.* (2008, 2009), heritabilities of 0·08 and 0·46 were estimated for agonistic interactions with weaned pigs. The heritabilities also had a wide range, which is in accordance with the heritabilities found in the present study. Løvendahl *et al.* (2005) estimated heritabilities for the agonistic behaviour of sows with values of 0·17–0·24 for IF and with 0·04–0·06 for RF. These results agreed with the heritabilities of the breeding gilts, which were also low for traits describing the aggressions received.

The literature suggests that agonistic interactions are related to reproductive traits. Tönepöhl *et al.* (2013) showed that sows which initiated more fights had more piglets in total and more piglets born alive. However, sows with fewer agonistic interactions cared better for their offspring (Løvendahl *et al.* 2005). Therefore, it seems that the traits NF ($h^2 = 0{\cdot}10–0{\cdot}18$) and IF ($h^2 = 0{\cdot}09–0{\cdot}13$) should be the priorities for improvement and will be discussed further in later publications.

Correlations between behavioural traits within different age groups

The NF trait showed high genetic and phenotypic correlations with all traits and within all age groups except for NF and FL in weaned pigs. Turner *et al.* (2008) estimated genetic correlations between number of fights and initiated fights of 0·79 in weaned pigs. These results are in accordance with the present findings. In weaned pigs, there were high genetic correlations between IF and FW as well as between RF and FL. Lower correlations were calculated between, in particular, IF *v.* FL and RF *v.* FW. Weaned pigs who initiated fights were more often

https://doi.org/10.1017/S0021859616000010 Published online by Cambridge University Press

the winners and the pigs which received most of the fights were more often the losers. The phenotypic correlations were similar for growing pigs and breeding gilts, but the genetic correlations were almost all high. The genetic correlations must be treated with caution since the small number of pigs in these two age groups and the low heritabilities can lead to an overestimation of the genetic relationships. The low estimates for the correlations between FL and FW could be explained by the statements of Rushen & Pajor (1987) that there is a balance between offensive and defensive interactions in pigs. These present results agree with the parameter estimation of Stukenborg *et al*. (2012) and Turner *et al*. (2008). They also found low correlations between the numbers of initiated and received fights. Another explanation for the correlations might be that pigs with standoffs were not considered in the traits FL or FW.

Correlations within behavioural traits between different age groups

Some contradicting genetic correlations were estimated between the age groups, which may be due to the small sample size and the small heritabilities for these traits. For the traits DF and FL between the ages, the estimations lead to no reliable results. Phenotypic correlations decreased as the difference in age increased. These results were in accordance with Stukenborg *et al*. (2012), who estimated phenotypic correlations between 0 and 0·47. The relationship also increased with smaller time differences between the age groups. This is not in accordance with the statements of Clark & D'Eath (2013), who argued that aggressive behaviour is a stable and consistent temperament trait of the individual pig. The genetic correlations were again much higher than the phenotypic and showed no general trend between the age groups.

CONCLUSION

The agonistic interaction of pigs at different ages showed that cross-fostering is an important effect, especially on the behaviour of weaned and growing pigs. Thus, cross-fostered animals are less aggressive than weaned and growing pigs. Hence, one explanation might be socialization in the early life of pigs, which leads to less aggressive behaviour in further mixing situations, whilst on the other hand the cross-fostered pigs may be less aggressive due to the decisive experiences of repeated defeats in fights after having been introduced to new litters. The agonistic interactions in weaned and growing pigs cannot be considered without regard to the weight of the pigs. The heavier the pigs, the more aggressive they are. The most important traits to describe agonistic behaviour in pigs are thus the number of fights and number of initiated fights with low to moderate but consistent heritabilities for all age groups. Also, the correlations between and across traits and age levels suggest that the number of fights and the number of initiated fights are the most suitable traits for the assessment of the agonistic interactions and the aggressiveness of pigs and should therefore be considered in further studies.

We thank the network of Phänomics for the financial support of this study.

REFERENCES

Chaloupková, H., Illmann, G., Pedersen, L. J., Malmkvist, J. & Simecková, M. (2008). Sow responsiveness to human contacts and piglet vocalization during 24 h after onset of parturition. *Applied Animal Behaviour Science* **112**, 260–269.

Champagne, F. A. & Curley, J. P. (2005). How social experiences influence the brain. *Current Opinion in Neurobiology* **15**, 704–709.

Clark, C. C. A. & D'Eath, R. B. (2013). Age over experience: consistency of aggression and mounting behaviour in male and female pigs. *Applied Animal Behaviour Science* **147**, 81–93.

D'Eath, R. B. (2004). Consistency of aggressive temperament in domestic pigs: the effects of social experience and social disruption. *Aggressive Behaviour* **30**, 435–448.

D'Eath, R. B. (2005). Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. *Applied Animal Behaviour Science* **93**, 199–211.

D'Eath, R. B. & Lawrence, A. B. (2004). Early life predictors of the development of aggressive behaviour in the domestic pig. *Animal Behaviour* **67**, 501–509.

D'Eath, R. B., Roehe, R., Turner, S. P., Ison, S. H., Farish, M., Jack, M. C. & Lawrence, A. B. (2009). Genetics of animal temperament: aggressive behaviour at mixing is genetically associated with the response to handling in pigs. *Animal* **3**, 1544–1554.

Erhard, H. W., Mendl, M. & Ashley, D. D. (1997). Individual aggressiveness of pigs can be measured and used to reduce aggression after mixing. *Applied Animal Behaviour Science* **54**, 137–151.

Fels, M. & Hoy, S. (2013). Einflüsse einer Gewichtssortierung von Aufzuchtferkeln auf Lebendmasseentwicklung, aggressive Auseinandersetzungen und Verletzungsgrad nach der Gruppierung (Effects of sorting weaner pigs by weight on growth performance, aggressive interactions and skin lesion score after mixing). *Berliner und Münchener tierärztliche Wochenschrift* **126**, 121–129.

Fraser, D. (1975). The teat order of suckling pigs: II. Fighting during suckling and the effects of clipping the eye teeth. *Journal of Agricultural Science, Cambridge* **84**, 393–399.

Fraser, D. & Jones, R. M. (1975). The teat order of suckling pigs: I. Relation to birth weight and subsequent growth. *Journal of Agricultural Science, Cambridge* **84**, 387–391.

GFE (2006). *Empfehlungen zur Energie und Nährstoffversorgung von Schweinen*. Frankfurt am Main, Germany: DLG-Verlag.

Groeneveld, E. (1990). *PEST User's Manual*. Neustadt, Germany: Institute of Animal Husbandry and Animal Behaviour Federal Research Centre.

Hurvich, C. M. & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika* **76**, 297–307.

Ismayilova, G., Oczak, M., Costa, A., Thays Sonoda, L., Viazzi, S., Fels, M., Vranken, E., Hartung, J., Bahr, C., Berckmans, D. & Guarino, M. (2013). How do pigs behave before starting an aggressive interaction? Identification of typical body positions in the early stage of aggression using video labelling techniques [in English]. Wie verhalten sich Schweine vor Beginn einer aggressiven Interaktion? Identifizierung typischer Körperpositionen im frühen Stadium aggressiver Auseinandersetzungen anhand von Video-Labelling-Techniken. *Berliner und Münchener tierärztliche Wochenschrift* **126**, 113–120.

Kovac, M. & Groeneveld, E. (2007). *VCE-6 User's Guide and Reference Manual Version 6*. Ljubljana, Slovenia: University of Ljubljana.

Langbein, J. & Puppe, B. (2004). Analysing dominance relationships by sociometric methods – a plea for a more standardised and precise approach in farm animals. *Applied Animal Behaviour Science* **87**, 293–315.

Litten, J. C., Drury, P. C., Corson, A. M., Lean, I. J. & Clarke, L. (2003). The influence of piglet birth weight on physical and behavioural development in early life. *Neonatology* **84**, 311–318.

Løvendahl, P., Damgaard, L. H., Nielsen, B. L., Thodberg, K., Su, G. & Rydhmer, L. (2005). Aggressive behaviour of sows at mixing and maternal behaviour are heritable and genetically correlated traits. *Livestock Production Science* **93**, 73–85.

Meese, G. B. & Ewbank, R. (1973). The establishment and nature of the dominance hierarchy in the domesticated pig. *Animal Behaviour* **21**, 326–334.

Otten, W., Puppe, B., Stabenow, B., Kanitz, E., Schön, P. C., Brüssow, K. P. & Nürnberg, G. (1997). Agonistic interactions and physiological reactions of top- and bottom-ranking pigs confronted with a familiar and an unfamiliar group: preliminary results. *Applied Animal Behaviour Science* **55**, 79–90.

Puppe, B. (1998). Effects of familiarity and relatedness on agonistic pair relationships in newly mixed domestic pigs. *Applied Animal Behaviour Science* **58**, 233–239.

Roehe, R., Shrestha, N. P., Mekkawy, W., Baxter, E. M., Knap, P. W., Smurthwaite, K. M., Jarvis, S., Lawrence, A. B. & Edwards, S. A. (2009). Genetic analyses of piglet survival and individual birth weight on first generation data of a selection experiment for piglet survival under outdoor conditions. *Livestock Science* **121**, 173–181.

Rushen, J. & Pajor, E. (1987). Offence and defence in fights between young pigs (*Sus scrofa*). *Aggressive Behaviour* **13**, 329–346.

SAS institute Inc. (2008). *User's Guide (Release 9.2)*. Cary, NC, USA: SAS Institute Inc.

Schwarz, G. (1978). Estimating the dimension of a model. *Annals of Statistics* **6**, 461–464.

Silerova, J., Spinka, M., Sarova, R. & Algers, B. (2010). Playing and fighting by piglets around weaning on farms, employing individual or group housing of lactating sows. *Applied Animal Behaviour Science* **124**, 83–89.

Stookey, J. M. & Gonyou, H. W. (1994). The effects of regrouping on behavioral and production parameters in finishing swine. *Journal of Animal Science* **72**, 2804–2811.

Stukenborg, A., Traulsen, I., Puppe, B., Presuhn, U. & Krieter, J. (2011). Agonistic behaviour after mixing in pigs under commercial farm conditions. *Applied Animal Behaviour Science* **129**, 28–35.

Stukenborg, A., Traulsen, I., Stamer, E., Puppe, B., Presuhn, U. & Krieter, J. (2012). Heritabilities of agonistic behavioural traits in pigs and their relationships within and between different age groups. *Livestock Science* **149**, 25–32.

Tan, S. S. L., Shackleton, D. M. & Beames, R. M. (1991). The effect of mixing unfamiliar individuals on the growth and production of finishing pigs. *Animal Production* **52**, 201–206.

Tönepöhl, B., Appel, A. K., Voß, B., König Von Borstel, U. & Gauly, M. (2013). Interaction between sows' aggressiveness post mixing and skin lesions recorded several weeks later. *Applied Animal Behaviour Science* **144**, 108–115.

Tuchscherer, M. & Manteuffel, G. (2000). Die wirkung von psychischem stress auf das immunsystem. Ein weiterer grund für tiergerechte haltung (übersichtsreferat). *Archiv Tierzucht* **43**, 547–560.

Tuchscherer, M., Puppe, B., Tuchscherer, A. & Kanitz, E. (1998). Effects of social status after mixing on immune, metabolic, and endocrine responses in pigs. *Physiology and Behavior* **64**, 353–360.

Turner, S. P., Roehe, R., Mekkawy, W., Farnworth, M. J., Knap, P. W. & Lawrence, A. B. (2008). Bayesian analysis of genetic associations of skin lesions and behavioural traits to identify genetic components of individual aggressiveness in pigs. *Behavior Genetics* **38**, 67–75.

Turner, S. P., Roehe, R., D'eath, R. B., Ison, S. H., Farish, M., Jack, M. C., Lundeheim, N., Rydhmer, L. & Lawrence, A. B. (2009). Genetic validation of postmixing skin injuries in pigs as an indicator of aggressiveness and the relationship with injuries under more stable social conditions. *Journal of Animal Science* **87**, 3076–3082.

Turner, S. P., Farnworth, M. J., Mendl, M., Erhard, H. W. & Lawrence, A. B. (2011). Evidence for residence-induced enhancement of aggressiveness in the non-territorial pig. *Applied Animal Behaviour Science* **130**, 10–19.