

Title: Using Behavioral and Genomic Tools to Identify Pigs Suited for Group Living,
NPB #14-066

Investigator: Janice Siegford

Institution: Michigan State University

Co-Investigators: Juan Steibel, Ronald Bates, Catherine Ernst, Simon Tuner & Madonna Gemus-Benjamin)

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Industry Summary:

In pigs, social behaviors, such as fighting, can affect the performance of all pigs in a group or result in injury or lameness, leading to culling. Expanding genetic selection programs beyond production and health traits to encompass behavior will improve welfare and productivity for group-housed pigs, particularly gestating sows. This study compiled behavioral, genomic, and production data from over 4,000 pigs to better understand the potential for selecting for pigs that are behaviorally adapted for group housing without compromising other traits of interest. We have characterized key aggressive behaviors of pigs in group-housing environments at the nursery, finisher and breeding stage and related these responses to measures of productivity and genetic components for application in breeding programs. Pressing behavior between pigs leads to damaging aggression in a majority of instances, suggesting it could be used as reliable predictor of physical aggression. Immediate prior social experience but not relatedness alone reduces aggression between pigs as they move from the nursery to finisher stage. Social aggression does not appear to be related to fear responses of pigs, nor to their response to human approach or backfat. Aggression, as assessed using lesion scores, is variable between pigs with respect to levels and types of aggression pigs show. Packages and programs have been developed to facilitate genetic analysis of behavioral and performance data, along with improved models for estimating indirect genetic effects. Together the findings and tools generated from the project can be used to improve selection models used in the swine industry to breed pigs better suited to modern husbandry environments, which will enhance the sustainability of pork production in Michigan and the U.S.

Contact information for Dr. Janice Siegford: email = siegford@msu.edu, phone = 517-432-1388.

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For more information contact:

National Pork Board • PO Box 9114 • Des Moines, IA 50306 USA • 800-456-7675 • Fax: 515-223-2646 • pork.org

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Scientific Abstract:

A welfare concern for group-housed pigs is aggression, particularly in the first 24 h following re-grouping with new individuals. This study characterized social behaviors of pigs in group-housing environments, related behavioral responses to health and productivity and identified genetic components associated with key behaviors for application in breeding programs. Data were collected from 1,092 purebred Yorkshire pigs. Pigs were strategically mixed into new groups at 3 ages: weaning (~27 d of age), move to finisher pens (~72 d of age), and at approximately 100 kg (~150 d of age, gilts only). Total number of fresh lesions (< 24 h old, bright red marks on skin) were counted prior to mixing (baseline), 24 h post mixing, and 3 wk post mixing. Video recordings made immediately and 3 wk after mixing were decoded to characterize behavior. Pigs were genotyped using a 70k SNP chip (Neogen Corporation – GeneSeek Operations). Phenotypically, pigs show different levels and types of aggression. Further, aggression as measured using lesion scores, is heritable, (0.17 - 0.46); thus selection against undesirable aggressive phenotypes is possible. Pigs housed with each other in the nursery prior to moving to a new group in the finishing stage displayed 2.62 times less fighting compared to unfamiliar animals ($P < 0.01$). Fights and one-sided attacks follow body-pressing events between two pigs in 75% of observations ($P < 0.01$); thus, pressing can be used to predict damaging aggression. Fear tests on a subset of barrows ($n = 257$) found no relationship between measures of fear (i.e., latency to approach or touch a novel object) and lesion scores ($P > 0.15$). Fear and inter-pig social aggression may be regulated by different processes, enabling selection against aggression without affecting fear response. Analysis of a subset of gilts ($n = 270$) suggested no relationship between lesions and backfat ($P = 0.584$) or between backfat and interactions with humans ($P = 0.607$). There was also no relationship between lesions and total interactions with humans ($P = 0.509$) or with total number of bites ($P = 0.196$). Thus, for this group of Yorkshire gilts, leaner pigs were not necessarily more aggressive than pigs with more fat, and pig-pig aggression was not related to the how pigs interacted with humans. In addition to generating data related to phenotypic expression and underlying genetic components of aggression, several statistical programs and packages have been developed for genetic analysis of behavioral data. These facilitate fitting of models, perform genome-wide association studies, and summarize and graphically present behavioral data from decoded videos. We are combining our data with existing data from 2 additional groups of pigs in a meta-analysis. We will also complete genome-wide association studies to identify regions within the genome responsible for the observed variation. In summary, aggression is variable among pigs and heritable, but does not appear to be directly related to fearfulness, response to humans, or to leanness, suggesting that selection against aggression should not negatively impact these traits. However, our results and previously published findings indicate that it is not as simple as selecting against all aggression, but that selection must be targeted in ways that does not affect long-term group stability.

Introduction:

Problem Statement

The US pig industry is currently undergoing the most significant shift in production practices since the middle of the 20th century as it transitions from individual housing to group housing of gestating sows. A combination of legislative actions in some states, along with customer purchasing decisions is driving this change. Recently, numerous retailers and food service chains that purchase or distribute pork products including McDonald's, Oscar Mayer, Kroger and Sysco announced they will require their suppliers to transition to group housing for gestating sows. Depending on the legislation or company, the pork industry must implement changes to sow housing between 2017 and 2022.

This change is not simply a matter of changing physical housing systems by replacing individual sow stalls with group pens. Genetic selection decisions in the pork industry over the past several decades have focused on production traits assessed on an individual animal basis. However, there is growing evidence that sows selected on this basis do not function or perform well in a group-housing environment.

Significance

Pigs are naturally social animals. In the wild or feral state, they tend to cohabit in bands of a few closely related females and their offspring. Aggression is infrequent, and when it does arise it is typically limited to mating periods, or disputes related to food sources or preferred lying places. To avoid aggression, pigs in the wild will develop a social order and maintain a certain distance between each other, as well as use threats or nonaggressive behaviors to maintain dominance relationships. Pigs in modern production systems tend to be grouped-based on functional characteristics rather than kinship. Further, these groups typically change over time. In these situations, aggressive flare-ups are common and often cause injuries and stress.

Group housing of gestating sows will increase the number of times that a sow is mixed with other animals, necessitating repeated establishment of social hierarchies among cohorts. The modern pig is not well adapted for this significant management change. A limited number of behavioral phenotypes have been evaluated for pigs in group settings, and these have been shown to have low to moderate heritabilities, and thus should respond to selection. However, very little research has considered the repeatability of behavioral traits in group-housed pigs following repeated mixing with different cohorts. In addition, most studies to date have focused on negative behaviors primarily related to fighting and aggression, with little attention to positive social interactions among pigs that could facilitate group living. Our research bolsters the limited information available to pork producers as they make selection, housing and management decisions related to group housing of gestating sows.

Background

Sows mixed with unfamiliar females fight for 2-7 days after mixing, and this occurs each time sows are mixed across subsequent parities. In grower pigs, it may be several weeks before the number of fresh skin lesions that result from fighting returns to pre-mixing levels (Turner et al., 2013). Previous research on fattening pigs indicates that fighting behavior in pigs is moderately heritable ($h^2 = 0.31$ to 0.47 , Turner et al., 2008, 2009; D'Eath et al., 2009). Skin lesion counts, which serve as an indicator trait for aggressive

behavior, are also heritable ($h^2 = 0.12$ to 0.26 , Turner et al., 2008, 2009) and are genetically correlated with aggressive behavior ($r_g = 0.56$ to 0.79 , Turner et al., 2008, 2009). Further, aggressiveness plays a role in the heritable effect that each pig has on the productivity of its penmates (Canario et al., 2012). Lovendahl et al. (2005) observed aggressive behavior in sows after mixing and also found moderate heritabilities ($h^2 = 0.17$ to 0.24), as well as a negative relationship with maternal behavior ($r_g = -0.3$), suggesting that selection against aggression is possible without harming maternal behavior. Similarly, Hellebrugge et al. (2008) reported a h^2 of 0.32 for aggressiveness of sows when regrouped, although aggressiveness was positively correlated with responsiveness to separation from piglets during the first 24h after birth ($r_g = 0.4$). However, less aggressive sows tended to have lower piglet mortality due to crushing.

Most programs that predict genetic merit assume an additive genetic model with no interactions among genotypes. However, if social interactions affect individual responses to selection, such an assumption is not valid and observed selection responses could be less than expected if selection is based only on additive genetic models (Muir, 2005). Social genetic effects, or indirect genetic effects, are heritable effects that an individual has on the phenotype of its group mates or social partners. Inclusion of indirect genetic effects into breeding programs takes into account both the additive genetic merit of an individual for its own performance (i.e., the direct genetic effect) and its indirect genetic effect on the performance of its group mates. Social effects contribute a large proportion of the genetic variance in pig growth rate (Bergsma et al., 2008; Chen et al., 2009; Canario et al., 2012). Canario et al. (2012) summarized direct breeding values (DBV) and social breeding values (SBV) into a total breeding value (TBV) for average daily gain from 35 to 100 kg BW. Selection for TBV using this approach could promote rapid establishment of dominance relationships with more initial aggressive contests at mixing, but less fighting in a stable social situation. A recent study examined offspring of pigs that had been selected for either high or low growth indirect genetic effects and housed in homogeneous groups (Camerlink et al., 2013). Aggression appeared to be reduced by this selection strategy in a manner indicating the pigs may have formed more stable dominance relationships. Thus, the authors concluded that it was likely that selection for growth indirect genetic effects targeted a behavioral strategy rather than a single behavioral trait, such as aggressiveness.

Few studies have considered associations between molecular markers or genomic loci and pig behavior traits, but none have looked at groups of pigs (Désautés et al., 2002; Muráni et al., 2010; Wilson et al., 2012). A few significant QTL have been identified for some behavioral traits associated with young pigs' response to novel environment and others related to elements of the hypothalamic-pituitary-adrenal axis associated with the stress response (Désautés et al., 2002). More recently, the genes NR3C1 and AVPR1B have been found to exhibit strong association with stress responsiveness and aggressive behavior (Muráni et al., 2010).

Thus, only limited work linking social behavior to molecular genotypes has been reported in pigs. No studies have yet examined whether favorable social behaviors are heritable and could be selected for as another avenue to minimize aggression and facilitate living in groups. In this proposal, we evaluated social behaviors of pigs at mixing and under more stable social conditions to better understand how these behaviors can ultimately reduce culling and losses from growing pigs and in sow herds with a cutting edge integrated genomics approach.

This project evaluated a comprehensive set of behavioral phenotypes in group-housed pigs at three time points during their development. Aggressive behavior of pigs has been compared with other aspects of temperament such as fear and response to human approach and handling as well as to backfat. Concurrently, DNA samples from pigs were collected for genomic analysis in order to begin to associate behavioral phenotypes with genotypes. Data collected from finishing pigs at MSU were supplemented by data previously collected by colleagues at Scotland's Rural College (SRUC; Edinburgh, Scotland) to improve the power of the analysis. This innovative approach will have a significant impact on research efforts for identifying the effects of group housing on pigs. The project has generated basic knowledge that can be translated to the pork industry to optimize genetic selection programs with the inclusion of animal behavior traits to improve adaptation to group housing of gestating sows.

Overall Goal

Our **overall goal** is to help ensure the sustainability of pork production by improving producer's ability to use animal behavior in breeding programs to improve welfare and productivity of group-housed pigs, particularly of gestating sows. Social behaviors, such as fighting, can affect the performance of all pigs in a group or result in injury or lameness, leading to culling. We characterized social behaviors of pigs in group-housing environments, related behavioral responses to health and productivity and identified genetic components associated with key behaviors for application in breeding programs.

Objectives

Objective 1: Conduct a comprehensive social behavioral assessment of group housed pigs after mixing into new social cohorts at three different ages, examining immediate responses to mixing and to stable social situations.

Objective 2: Estimate genetic parameters and perform genome-wide prediction and association of social behavioral traits expressed by group-housed pigs to determine underlying genomic control of these traits.

Materials & Methods:

Animals

The following data were collected experimentally at MSU (Population 1) at 3 ages, and combined with existing data exist from 2 additional, unrelated commercial groups of pigs (Populations 2 and 3). *Population 1:* 1,092 purebred Yorkshire pigs were produced and housed at MSU in a series of 8 replicates. Each replicate consisted of male and female piglets from single sire litters (~140 pigs/replicate) with known pedigrees. *Population 2:* 2,484 pigs of Large White, Landrace and Duroc derivation studied at a pedigreed commercial PIC unit in 8 replicates of 9 pens each (138 pens in total) of 18 pigs/pen. *Population 3:* 1,663 pigs (898 purebred Yorkshire and 762 crossbred Yorkshire × Landrace), studied at a genetic nucleus unit, were the progeny of 85 sires and 250 dams and were housed in 111 pens of 15 pigs/pen.

Animal-Based Measures

Population 1. Behaviors were monitored at three ages when pigs are commonly mixed into new social cohorts: 1) weaning (~5 kg body weight (BW), 10 pigs/pen), 2) movement into grow-finish facilities (~23 kg BW, 14 pigs/pen) and 3) at sexual maturity when gilts are placed into the breeding herd (~90 kg BW, 14 pigs/pen). Blood samples were collected from each animal to obtain DNA for genomic analyses (Objective 2). Prior to mixing, the number of injuries (fresh skin lesions) on each pig were counted following methods developed at SRUC (Figure 3; Turner et al., 2006), who demonstrated that skin lesions, and their location, are a reliable biomarker for quantifying aggression. Each pig was evaluated for lesions by body region: front (head, neck, shoulders and front legs), middle (flanks and back) and rear (rump, hind legs and tail). The number of fresh lesions were counted for each region and totaled. Non-toxic livestock marker was used to mark each pig for easy individual identification. Video cameras and infrared lights were installed above the pens and connected to a multichannel digital video recorder to allow for recording with and without supplemental lighting. After each mixing event, the behavior of the pigs was recorded for 24 h. After 24 h, skin lesions on each pig were recounted and the number of lesions recorded at 24 h was subtracted from the initial value (Turner et al., 2006). Three weeks after each mixing event, skin lesions were counted again and another 24 h of continuous video recorded. Data collected immediately after mixing demonstrate pigs' response to social change, while data collected 3 weeks later provide information on the pigs' social behavior in a familiar, stable group. Approximately one week after mixing at ~90 kg, pigs in Population 1 were weighed in pen cohorts to determine growth rate to a common age and backfat thickness and loin muscle area were estimated using B-mode ultrasound. Onset of puberty was recorded for gilts in Population 1. An intact male was introduced to each pen daily and record made of gilt's age in days when she stood to be mounted by the boar.

Populations 2 & 3. Animals in both Populations 2 and 3 were mixed into new social groups when moved into grow-finish pens at a similar weight to the second mixing proposed for Population 1 (~23 kg). Existing data for Populations 2 and 3 to be used in the current proposal was as follows. *Population 2:* skin lesions were recorded for 2,484 pigs at mixing and 3 wk later using the protocol described for Population 1 (above), and SNP genotypes were obtained for all 2,484 pigs using a 60K SNP chip or imputed from a smaller panel. *Population 3:* skin lesions were recorded for 1,663 pigs at mixing and 3 wk later using the aforementioned protocol, along with detailed aggressive behavioral phenotypes from 1,168 of these pigs as described for Population 1 (below) and 62K SNP data for 552 pigs. Weight at finishing, backfat thickness and meat quality were also available from Populations 2 and 3.

Analysis of Behavior from Video

Social interactions and their outcomes were recorded using protocols already developed during the previous analysis of Population 3 (Turner et al., 2009). Duration of aggressive behavior, including one-sided attacks and reciprocal fighting between pigs were recorded, together with initiator and winner identities. Due to the position of cameras and lighting in the rooms, it was not possible to differentiate between tail and vulva biting, and ear biting was observed too rarely to allow be analyzed. Recording of positive social behaviors and behaviors of pigs that might minimize aggression, such as turning the head away or walking away from another pig, is ongoing.

Genetic Analysis of Behavioral Traits

Behavioral trait phenotypes for Populations 1, 2 and 3 were used. For Population 1, 1,082 pigs were successfully genotyped at GeneSeek (Lincoln, NE) using the Illumina SNP70 chip. Genotype data from 60,000 SNP marker (60K SNP) panels were available from previous studies for Populations 2 and 3.

The genetic analysis was comprised of two parts that are essential components of studies of genetic architecture of any trait or group of traits (Hayes et al., 2010). In Objective 2a, we determined the potential for genetic selection for the traits of interest (Goddard et al., 2011). In Objective 2b, we determined specific genomic regions controlling phenotype expression, which is a first step in finding causative variants (Ernst & Steibel, 2013). We used a single genomic model for both goals, genetic parameter estimation and GWA, which pivots around computation of a genomic relationship matrix.

Estimation of genomic relation and genetic parameters

A key part of our methodology revolves around the construction of the genomic relationship matrix \mathbf{G} (VanRaden, 2008). Following VanRaden (2008), we first standardized the marker matrix \mathbf{Z} by subtracting the expected allelic dosages ($2p_i$) for each SNP and dividing by a common expected variance of allelic dosages $\sqrt{2 \sum p_i(1-p_i)}$. Second, we multiplied \mathbf{Z} by its transpose to compute $\mathbf{G} = \mathbf{Z}\mathbf{Z}'$. This N -by- N matrix will contain estimates of the realized genomic relationship between any two animals. For genetic parameter estimation, we will build a population-specific relationship matrix. Subsequently, we will fit a classic animal model that will include fixed effects (e.g. year-season, pen, sex, etc.), random animal effects and residual effects. For those traits that are non-continuous (e.g., count-based traits) we will either transform the variable, which should work for traits where the number of counts is relatively large and where there is no zero inflation (too many zeros), or when counts are very small and may contain many zeros, we will use models with distributional properties that best fit the data (as in Vazquez et al., 2009). After fitting these different models, estimates of variance components will be used to compute heritabilities. Multi-trait extensions of the previously discussed models will be used to estimate genetic correlations (Hayashi and Iwata, 2013).

Testing for association

The estimated animal breeding values from the previous model were transformed into regularized marker effects with a simple linear transformation following Wang et al., (2012). Likewise, the variance covariance matrix of the estimated marker effects was computed from the mixed model equations of the animal model. Manhattan plots of marker effects were constructed by plotting the estimated marker effects divided by the square-root of their variance versus the genomic position. We then used Manhattan plots to detect peaks of standardized marker effects as illustrated in our previous work.

Incorporation of social and direct genomic effects

We expanded the previously described models to incorporate social effects in addition to direct genomic effects following Bergsma and colleagues (2008). An important issue in these types of models is to avoid the confounding of pen effect and social group interaction (Cantet and Cappa, 2008). In our case we avoided confounding in two ways: 1) by design, using the mixing scheme that resulted in the same animal being part of several social groups over time and 2) by addition of behavioral information. Cantet and Cappa (2008) have illustrated how behavioral observation can be used to break confounding of social groups with pen effects and we exploited the wealth of information obtained in Objective 1

to build covariance matrices based on observed social interactions. This modeling is completely new and original in the field of behavioral genetics. Moreover, the available molecular information helped incorporate relationships and better model covariances between direct and social effects.

Results: Report your research results by objective.

Objective 1: Conduct a comprehensive social behavioral assessment of group housed pigs after mixing into new social cohorts at three different ages, examining immediate responses to mixing and to stable social situations.

A subset of data from Population 1 has been analyzed to examine number of skin lesions (injuries) pigs would have before (pre), immediately after and 3 weeks (stable) following mixing into groups at three stages (nursery, finisher and replacement gilt (Wurtz et al., 2015a). Data analysis was performed by fitting a generalized over-dispersed Poisson mixed model. Fixed effects included phase of production (3 levels), observer (2 levels), sex (2 levels), measure (pre-mixing, post-mixing, and stable) and a live weight covariate. Random effects included animal ID, litter, and pen. Lesion counts by body location served as the response variable. As expected, lesion numbers were higher immediately after mixing for pigs of all ages, and stable scores returned to pre-mixing levels in nursery and replacement gilt groups (Table 1; Wurtz et al., 2015a). However, finisher pigs had higher numbers of lesions during the stable period compared to baseline numbers prior to mixing, though this difference was slight. Extensive variation was found in the number and location of lesions on the pigs’ bodies, indicating that pigs vary in both how aggressive they are and what types of aggression they may show.

Table 1. Differences of measure least squares means. Non-highlighted cells denote significance of $P < 0.01$. (Note: these numbers are presented as differences between least squares means to allow us to compare lesion scores while accounting for other terms in the model.)

		Post-pre	Pre-stable	Post-stable
Total	Nursery	1.875	-0.247	1.628
	Finisher	1.059	0.776	1.835
	Sow	2.084	0.014	2.098
Front	Nursery	1.797	0.012	1.809
	Finisher	1.355	0.343	1.699
	Sow	2.197	-0.080	2.117
Middle	Nursery	1.946	-0.567	1.380
	Finisher	0.906	1.071	1.978
	Sow	2.060	0.154	2.214
Rear	Nursery	2.021	-0.390	1.631
	Finisher	0.837	1.056	1.893
	Sow	1.914	0.014	1.928

To address concerns that selection against aggression might negatively affect production or alter how pigs interact with humans, data from half of the gilts from Population 1 (n = 270) were analyzed with respect to the relationship between aggression, backfat and pigs’

response to humans in their home pen (Jensen et al., 2016). Pigs' interactions with humans were assessed by having an observer enter the pigs' home pen for 9 min and record which pigs were biting, levering, or nosing the observer at 30-second intervals. A generalized linear mixed model was used to investigate the relationship between lesions and backfat and also between lesions and total interactions with humans. The fixed effects in the model were observer, repetition, and either backfat or number of human interactions. Pen was included as a random effect and weight was a covariate. The response variable was the number of lesions on the pig 24 h after being mixed into a new group at the finisher stage. Results suggested there was no relationship between lesions and backfat ($P = 0.584$) or between backfat and interactions with humans ($P = 0.607$). There was also no relationship between lesions and total interactions with humans ($P = 0.509$) or with total number of bites ($P = 0.196$). Thus, for this group of Yorkshire pigs, leaner pigs were not necessarily more aggressive than pigs with more fat, and pig-pig aggression was not related to the how pigs interacted with humans.

We have also begun to assess the importance of relatedness or prior experience on social behavior during mixing using a subset of data from Population 1 (Wurtz et al., 2015b). We investigated whether familiar pigs showed differences in aggression levels at mixing compared to unfamiliar pigs. Familiar pigs were defined as pigs that has been littermates or pigs that had been housed together in the nursery pens. Total time of reciprocal fighting was log transformed and fitted using a Gaussian mixed model with fixed effects of littermate and nurserymate, and random effects of pen and animal. Previous nurserymates displayed significantly less fighting compared to unfamiliar animals with unfamiliar pigs fighting 2.62 times more ($P < 0.0001$). Littermates tended to fight more with each other than with non-littermates ($P = 0.099$). However, this result may be an artifact of small sample size and unbalanced data. We plan to continue to analyze this data as we progress through the data.

Data from pigs of Population 1 in the finisher phase of have been examined to determine whether non-damaging physical interactions, such as pressing, predict whether damaging aggression will follow. Multinomial logistic regression using PROC GLIMMIX in SAS was performed to examine the likelihood of each aggressive behavior to occur after either parallel pressing or inverse parallel pressing. Inverse parallel pressing (i.e., pigs standing head to tail and pressing their bodies against each other) and parallel pressing (i.e., pigs standing head to head and pressing their bodies against each other) occur frequently between newly mixed pigs. Reciprocal fights between pigs or one-sided attacks followed pressing events in 75% of observations ($P < 0.01$; Alves da Cunha Valini et al., 2015). Thus, pressing can be used to predict damaging aggression.

We began to explore the relationship between social aggression and other behavioral traits, such as personality and fear response to novelty, using a novel object test with 257 4-month old barrows in stable groups. We used a principal component analysis to understand the relationship between the recorded novel object test variables (latency to cross the 0.5 m and 1m lines, latency to touch the novel object, number of times crossing the 0.5 m and 1 m lines, number of times touching the novel object, and number of vocalizations made during the test).

PC1, which explained 71% of the variance, had a high loading for latency to touch the novel object, which was positively loaded with latency to reach both the 0.5 m and 1 m lines

(Table 2). Thus, the slower a pig was to cross the lines, the slower it was to touch the novel object, as well. PC3 explained 10% of the variance, and also had strong loadings for the latency variables, though the relationship between them was different than for PC1. PC3 describes the situation where pigs were fast to reach the 0.5 m or 1 m lines but then slow to touch the novel object. Vocalization was the only variable loading strongly on PC2, and this component explained 16% of the variance.

Table 2. Results of a principle component analysis examining the relationships among variables in the novel object test.

	PC1	PC2	PC3
Latency to 1 m	0.39	0.05	-0.59
Latency to 0.5 m	0.59	-0.02	-0.42
Latency to Touch	0.70	-0.11	0.68
# 1 m Crosses	-0.01	-0.01	-0.01
# 0.5 m Crosses	-0.01	-0.003	0.003
# Touches	-0.01	0.01	-0.01
#Vocalizations	-0.06	-0.99	-0.09
Variance Explained	71%	16%	10%

To identify individual variation in pigs' response to a novel object, a cluster analysis was performed using the latency variables as these had explained the majority of variance in the principle component analysis. This analysis identified three groups within the population (Figure 1, Table 3). Cluster 1 was composed of pigs that were both slow to approach the lines and slow to touch the novel object; this group corresponds to the relationship described by PC1. Cluster 2 pigs were relatively quick to approach the lines in comparison, but then waited before touching the ball, as described by PC2. Cluster 3 pigs were quick to approach both lines and touch the ball.

Table 3. Results of a cluster analysis examining the relationships among variables in the novel object test.

Cluster	# Pigs	Lat 1 m (sec)	Lat 0.5 m (sec)	Lat Touch (sec)
1	29	163.7	251.5	261.6
2	61	52.3	92.7	169.9
3	167	19.6	25.3	32.3

Finally, to explore the relationship between social aggression and fear response to novelty, a generalized linear mixed model was fit to the data (O'Malley et al., 2016) using total number of lesions 24 h after mixing as the response variable, weight at mixing as a covariate, and home pen as a random effect. The fixed effects were latency to 1 m line, latency to 0.5 m line, latency to touch the novel object, pre- and post-lesion scorer, and repetition. Novel object test variables were unrelated to skin lesion scores: latency to 1 m

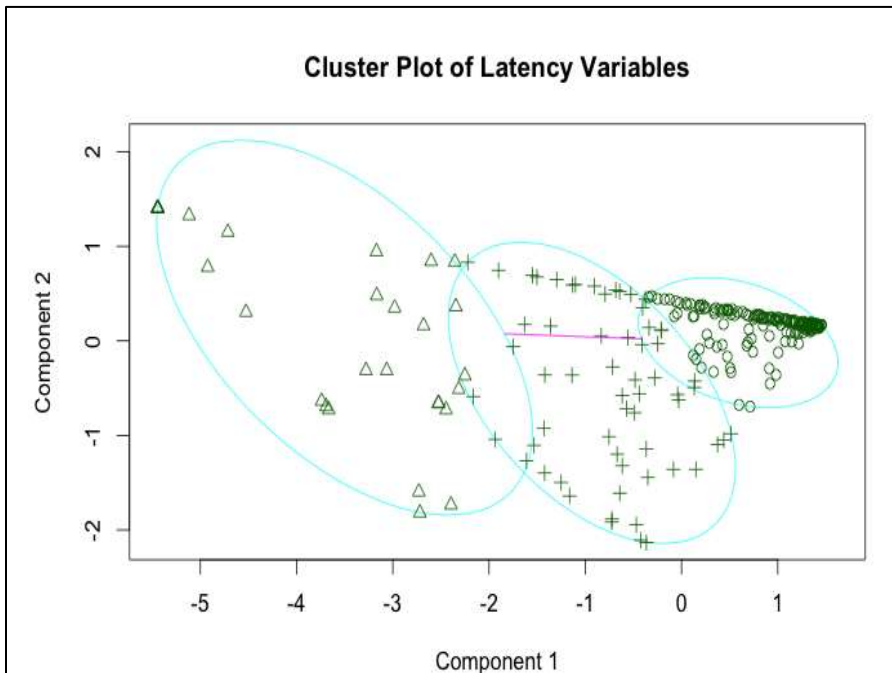


Figure 1. Plot of latency response variables from a novel object test conducted with 4-month old barrows in stable social groups. The two components explain 95.03% of the point variability.

line ($P = 0.15$), latency to 0.5 m line ($P = 0.58$), and latency to touch ($P = 0.89$). The results suggest that though pigs may show distinct types of responses to the novel object, there is no relationship between fear response to a novel object and social aggression. Therefore fear and inter-pig social aggression may be regulated by different biological processes.

Objective 2: Estimate genetic parameters and perform genome-wide prediction and association of social behavioral traits expressed by group-housed pigs to determine underlying genomic control of these traits.

Programs and packages for genetic analyses of behavioral and performance data: We have developed the gwaR package (<https://github.com/steibelj/gwaR>) that allows efficient fitting of GBLUP models and performance of GWA following our previously published methods (Bernal Rubio et al., 2016; Gualdrón Duarte et al., 2014). In our current version we have a function for fitting linear mixed models: `gblup(rsp,data,design,G,vdata = NULL, wt = NULL)`, where `rsp` indicates the name of the response variable, `data` contains phenotypic and covariate information, `G` is the input relationship matrix and `vdata` and `wt` allow parsing information on additional covariance matrices and weights (these are useful to analyze de-regressed breeding values, for instance). We also developed a function to perform GWA: `gwas(gb, x)` where `gb` is the output of the `gblup` function and `x` is a genotype matrix. This package can efficiently analyze data from 1000s of animals and 100s of 1000s of SNP and produce summaries of results for estimated genetic parameters and genome-wide association, including graphics and descriptive summaries. To specifically fulfill the goals stated in this proposal, we adapted functions of our package gwaR to perform bivariate analyses. To this end we created two more functions that allow estimating the genetic and environmental correlations between lesion scores measured at different periods or in different body locations and we estimated genetic and phenotypic correlations between lesion scores.

We also developed a function to summarize behavioral data decoded from the existing videos. Assuming that decoded video data comes in the format described in Table 4, we developed a function to compute the total time spent by any two animals interacting with each other.

Table 4. Data resulting from decoding video data. Each row corresponds to a single interaction. Behavior codes correspond to HK= Head Knocking, IP= inverse parallel pressing, PP= parallel pressing, AT= attack, B= single bite.

Observer	Date	Start Time	End Time	Pen	PigID	Behavior code	Fight initiator	Fight Winner
LJ	11/6/2014	16:29:48	16:29:49	F4-13	8,2	HK	8	
LJ	11/6/2014	16:34:06	16:34:07	F4-13	12,3	B		
LJ	11/6/2014	16:36:31	16:36:38	F4-13	13,3	IP		
...
LJ	11/6/2014	05:18:10	05:18:14	F4-13	5,2	AT	5	5
LJ	11/6/2014	05:18:15	05:18:31	F4-13	5,3	PP		

The input and output of the function `inter.mat` is described below.

`inter.mat(input,format_options,coding_options,filtering_options)`

In this function, parameter `input` represents a pointer to a file containing records of social interactions as described in Table 1. `format_options` is a parameter needed to give flexibility to different input files, such as variable names, type of data stored, etc; `coding_options` gives basic information about the ethogram or any coding that was used to classify interactions and `filtering_options` is a set of parameters where basic rules for data editing and flagging can be specified. The output from this function is a list that includes slots for estimated interaction matrices and animal-specific information. The interaction matrix is a square symmetric matrix of dimension equal to the number of animals in the social group; each element of the matrix is a value representing the time spent by two animals interacting with each other. The animal-specific information is stored in a vector and it is the total number of seconds that an animal spent interacting with any other animal. This vector is not simply the sum of the elements in a row or column of the interaction matrix, because there may be three and four way interactions that when reduced to pairwise data and summed over all possible pairs of animals may result in overestimating total fighting and interaction times.

In addition to this core function, we have also developed functions for summarizing and graphically presenting the output from `inter.mat`. For instance, interaction matrices can be presented as a network graph (Figure 2), where each node represent an animal in the social group and the thickness of the edge is proportional to the time two animals spent interacting.

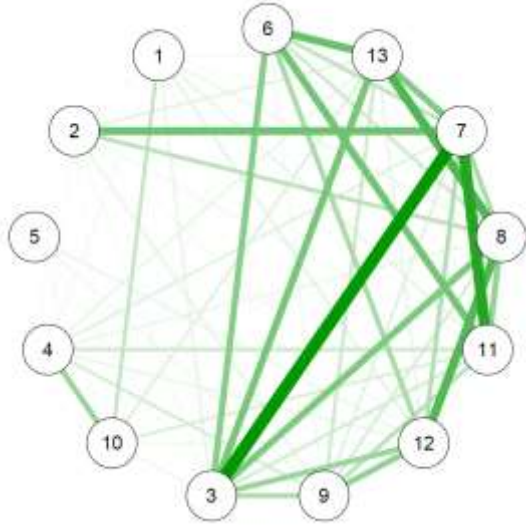


Figure 2. Network representing an interaction matrix. Thirteen nodes in the network represent animals composed this social group, the thickness and intensity of the each edge connecting two nodes is proportional to the number of seconds that two animals spent interacting with each other.

Finally, output from the `inter.mat` function can be used as response variable in a number of analyses such as the examination of prior social experience with a pig or relatedness (Wurtz et al., 2015b).

Preliminary genetic analysis for lesion scoring and other phenotypes: Phenotypic records have been collected and pigs from the MSU population have been genotyped with a 70K SNP chip. In a first analysis,

genotypes for 560 pigs were used to compute the genomic relationship matrix and phenotypes were analyzed with the following model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{u} + \mathbf{Z}_p\mathbf{p} + \mathbf{e},$$

where \mathbf{y} is a $n \times 1$ vector of records, \mathbf{X} is a full rank $n \times p$ incidence matrix relating the observations to fixed effects included in vector $\boldsymbol{\beta}$: sex, replicate, observer, initial weight (weight at mixing), and lesion count pre-mixing, \mathbf{u} is the vector of direct breeding values, \mathbf{Z}_p is the incidence matrix relating records to pen effects \mathbf{p} . We made classic distributional assumptions: $\mathbf{e} \sim \mathbf{N}(\mathbf{0}, \mathbf{I}\sigma_e^2)$, $\mathbf{p} \sim \mathbf{N}(\mathbf{0}, \mathbf{I}\sigma_p^2)$, $\mathbf{u} \sim \mathbf{N}(\mathbf{0}, \mathbf{G}\sigma_u^2)$. All analyses were performed using our software package `gwaR`. We estimated all variance components and heritabilities (Table 2).

Table 2. Preliminary estimates of genetic parameters. Trait description: L.S: log(Lesion scores+1) measured at several periods. Only post-mixing counts are reported. W.G: weight gain in several periods, LEA: loin eye area (measured once), BF: backfat depth (measured once).

L.S.	Nursery			Finisher			Sow		
	σ_e^2	σ_p^2	h^2	σ_e^2	σ_p^2	h^2	σ_e^2	σ_p^2	h^2
Front	0.66	0.07	0.27	0.57	0.06	0.37	0.49	0.05	0.46
Middle	0.72	0.07	0.21	0.67	0.13	0.20	0.79	0.04	0.17
Rear	0.59	0.18	0.24	0.59	0.23	0.18	0.65	0.01	0.34
W.G.	31.05	2.09	0.39	136.96	5.07	0.32	-	-	-
LEA	-	-	-	11.14	0.79	0.39	-	-	-
BF	-	-	-	0.04	0.00	0.71	-	-	-

These estimates of genetic parameters are very similar to those reported by our collaborators using larger populations and pedigree based relationship matrices, including using the large SRUC dataset described above (Desire et al., 2015; Turner et al., 2009). This demonstrates our capacity to effectively process phenotypic and genotypic data and to produce estimates of genetic parameters for complex behavioral traits.

Through fitting bivariate models, we found that genetic correlation were in general much stronger than phenotypic correlations (Wurtz et al., 2016). For instance, genetic correlations between measures in different body locations were always above 0.83, but phenotypic correlations were less or equal to 0.75 (Wurtz et al., 2016). A similar pattern

was observed for correlations of lesion scores between growth stages, but the magnitude was smaller, for instance: genetic correlations ranged between 0.55 and 0.8 while phenotypic correlations were between 0.04 and 0.32. Although these results are preliminary due to the small sample size (i.e., only half of Population 1 has thus far been analyzed in this way), it reaffirms that out sampling design allows for estimation of genetic parameters and that our team can carry out all proposed genetic analyses.

Discussion:

The results of our initial analysis comparing lesion counts for different areas of the body at different ages were made indicated that there was extensive variation in skin lesions that could be modeled and attributed to systematic factors (Wurtz et al., 2015a). This variation shows potential for use in genetic analysis. This study also highlighted the possibility of using the difference between post and pre lesions as an additional response variable to select on accumulation of lesions post mixing. As expected, when mixed into new groups, pigs coming from the same previous social group fought less with each other than with other pigs (Wurtz et al., 2015b). Surprisingly, there was a tendency for littermates that were not also penmates in the nursery phase to fight more; however, this result was likely an artifact of having a small number of such pigs compared to the group as a whole.

Results examining the relationship between aggression, backfat and gilts' response to humans suggest that leaner gilts were not necessarily more aggressive than pigs with more fat, and pig-pig aggression was not related to the how pigs interacted with humans (Jensen et al., 2016). These findings were similar to those found by Turner et al. (2006) and suggest that producers may be able to select for less aggressive animals without impacting an important trait of interest (i.e., leanness) or inadvertently selecting pigs that are more fearful or aggressive toward humans. Data from 270 barrows from the same population, including siblings of the gilts examined thus far, will be analyzed to add more power to these results. However, future research investigating other strains of pigs, including those with more variation in variation, is needed to confirm these results.

Heritabilities ranged from 0.17 to 0.46 for lesion scores (Wurtz et al., 2016), which are similar in magnitude to heritabilities of traits commonly selected for in industry. Genetic correlations of middle and rear lesions were extremely close to 1 suggesting that these could be treated as a single trait in future analyses. Consecutive stages had higher correlations than non-consecutive stages, however, correlations between the nursery and mature gilt stage for front and middle lesions were positively correlated suggesting the potential for selection decisions to be made at an earlier age. Further work is needed to perform analyses on a larger sample size and to examine stable group properties.

Previous studies focused on uncovering predictors of fights and attacks between pigs have noted that minor interactions, such as single bites, head knocks and shoves, happen before aggression escalates (D'Eath and Pickup, 2002). Pigs also tend to approach while facing each other before engaging in physical interactions leading to fights (Ismayilova et al., 2013). Our examination of non-injurious physical contact between pigs revealed that the majority of pressing events between pigs, in particular inverse parallel pressing, led to damaging aggressive interactions (Alves da Cunha Valini et al., 2015). These findings mirror those of other researchers who have shown that inverse parallel pressing is the most

common position assumed by pigs before a reciprocal fight or one-sided attack (Ismayilova et al., 2013; D'Eath and Pickup, 2002).

Previous work has shown that behavior at mixing is moderately heritable, with skin lesion heritability at 12-26%, and fighting behavior at 31-47%. It has also been shown that skin lesions are genetically correlated with aggressive behavior at 56-79% (Turner et al., 2006; 2008; 2009). Other work has shown that aggression is negatively correlated with good maternal behavior; therefore less aggressive pigs have lower piglet mortality (Lovendahl, 2005; Hellebrugge et al., 2008). The implication of these findings is that producers can breed for less aggressive pigs without impairing maternal behavior. Another concern from producers is that selection for less aggressive pigs could inadvertently heighten their fear response, and, as a result of being more fearful, pigs could show reduced feeding behavior, poorer maternal behavior, or be more difficult to handle. Thus, the goal of this portion of Objective 1 was to expand our understanding of how social aggression is related to the fear response to help ease the concern of producers, and so that we may better understand the impacts of selection on aggression on other traits. Though we did see distinct patterns in pigs' response to the novel object test, our results suggest no relationship between total skin lesions acquired after mixing and fear response (O'Malley et al., 2016). As we continue to analyze data from this study, we hope to look further into this relationship by looking at heritability of fear response.

Summary

Results of this project have revealed that aggression in pigs varies in phenotypic expression (i.e., pigs show different levels of types of aggression), and is heritable. Aggression does not appear to be directly related to fearfulness, response to humans, or to leanness, suggesting that selection against aggression should not have negative impacts on these traits. However, results of our study and previously published findings indicate that it is not as simple as selecting against all aggression, but that selection must be targeted in ways that does not affect long-term group stability. Ongoing meta-analysis of the data from the 3 populations of pigs in the study will provide additional power to our findings, and help us refine our modeling approaches and selection tools.

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Publications, Presentations, and Additional Funding Resulting from the Current Project

Published Peer-Reviewed Scientific Abstracts

- Jensen, L., C. O'Malley, S. Ison, K. Wurtz, J. Steibel, R. Bates, C. Ernst and J. Siegford. 2016. Is leaner meaner? The effect of leanness on pig-pig aggression and pig-human interactions in finisher gilts. *Proceedings of the 50th Congress of the International Society for Applied Ethology*. 50:146.
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Wurtz, K., C. O'Malley, J. Siegford, R. Bates, C. Ernst, N. Raney and J. Steibel. 2016. Estimation of heritability and environmental effects of number of scored lesions in group-housed pigs. *Proceedings of the 50th Congress of the International Society for Applied Ethology*. 50:89.

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Wurtz, K.E., J.P. Steibel, R.O. Bates, C.W. Ernst and J.M. Siegford. 2014. Using behavioral and genomic tools to identify pigs suited for group living. *Proceedings of the 12th ISAE North American Regional Meeting*, May 30-31, 2014 East Lansing, MI. p62.

Unpublished Presentations and Abstracts

Alves da Cunha Valini, G., C. O'Malley, K. Wurtz, J.P. Steibel and J.M. Siegford. 2015. Pressing as a predictor of agonistic interactions in confined pigs. *Animal Behavior and Welfare Group Research Presentation (with paper)*.

Wurtz, K., C. O'Malley, J. Siegford, J. Steibel. 2015b. Aggression and familiarity in pigs: does relatedness or recent social experience matter more? *Animal Behavior Society Annual Conference, June 10-14, Anchorage, AK*.

Invited Presentations

Siegford, J., J.P. Steibel, C. Ernst, R. Bates, S. Turner, R. D'Eath, and M. Gemus-Benjamin. 2016. Using behavioral phenotypes to improve genetic selection in pigs. *Purdue Animal Welfare Symposium*, West Lafayette, IN.

Siegford, J., J.P. Steibel, C. Ernst, R. Bates, S. Turner, R. D'Eath, and M. Gemus-Benjamin. 2016. Social phenotype and genotype selection for females to better suit group sow housing. *2016 Michigan Professional Pork Producers Symposium*, Lansing, MI.

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