

HOUSING AND MANAGEMENT

Estimation of direct and social effects of feeding duration in growing pigs using records from automatic feeding stations

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Abstract

Automatic feeding systems in pig production allow for the recording of individual feeding behavior traits, which might be influenced by the social interactions among individuals. This study fitted mixed models to estimate the direct and social effects on visit duration at the feeder of group-housed pigs. The dataset included 74,413 records of each visit duration time (min) event at the automatic feeder from 135 pigs housed in 14 pens. The sequence of visits at the feeder was employed as a proxy for the social interaction between individuals. To estimate animal effects, the direct effect was apportioned to the animal feeding (feeding pig), and the social effect was apportioned to the animal that entered the feeder immediately after the feeding pig left the feeding station (follower). The data were divided into two subsets: “non-immediate replacement” time (NIRT, $N = 6,256$), where the follower pig occupied the feeder at least 600 s after the feeding pig left the feeder, and “immediate replacement” time (IRT, $N = 58,255$), where the elapsed time between replacements was less than or equal to 60 s. The marginal posterior distribution of the parameters was obtained by Bayesian method. Using the IRT subset, the posterior mean of the proportion of variance explained by the direct effect ($Prp \hat{\sigma}_a^2$) was 18% for all models. The proportion of variance explained by the follower social effect ($Prp \hat{\sigma}_f^2$) was 2%, and the residual variance ($\hat{\sigma}_e^2$) decreased, suggesting an improved model fit by including the follower effect. Fitting the models with the NIRT subset, the estimate of $Prp \hat{\sigma}_a^2$ was 20% but the $Prp \hat{\sigma}_f^2$ was almost zero and $\hat{\sigma}_e^2$ was identical for all models. For the IRT subset, the predicted best linear unbiased predictor (BLUP) of direct (Direct BLUP) and social (Follower BLUP) random effects on visit duration at the feeder of an animal was calculated. Feeder visit duration time was not correlated with traits, such as weight gain or average feed intake ($P > 0.05$), whereas for the daily feeder occupation time, the estimated correlation was positive with the Direct BLUP ($\hat{r} = 0.51, P < 0.05$) and negative with the Follower BLUP ($\hat{r} = -0.26, P < 0.05$). The results suggest that the visit duration of an animal at the single-space feeder was influenced by both direct and social effects when the replacement time between visits was less than 1 min. Finally, animals that spent a longer time per day at the feeder seemed to do so by shortening the meal length of the preceding individual at the feeder.

Key words: feeding behavior, pigs, social effects

Abbreviations

AFI	average daily feed intake
BLUP	best linear unbiased predictor
Direct BLUP	BLUP of direct random effects
$elpd$	expected log pointwise predictive density
Follower BLUP	BLUP of social random effects
FOT	daily feeder occupation time
IRT	immediate replacement time
M1	statistical model 1
M2	statistical model 2
M3	statistical model 3
MCMC	Markov chain Monte Carlo
NIRT	non-immediate replacement time
Prp	variance proportion explained by each variance component
q	quantiles of the distribution
SGE	social genetic effect
WAIC	widely applicable information criterion
WG	animal weight gain

Introduction

In swine production, electronic feeding systems allow for the collection of individual feed intake, feeding behavior, and growth data of group-housed pigs (Young and Lawrence, 1994; Nielsen et al., 1995; Nielsen, 1999). The analysis of these records allows for the estimation of genetic and phenotypic parameters of feeding behavior and feed intake as well as their correlation with performance traits and their relation to systematic experimental factors (Hall, 1997; Chen et al., 2010; Lu et al., 2017). The analyses typically use classic animal models that include the random effect of the animal and different systematic effects, such as sex, age, batch, group size, and weight. However, in electronic feeding systems that provide only a single feeding space for all individuals in a group, feeding behavior traits may be affected by the presence of social interactions between individuals within the group; for example, competition for access to the feeder can modify feeding patterns, feed intake, and average daily weight gain (Nielsen et al., 1995; Manteca and Edwards, 2009). Thus, it is important to use models that allow joint modeling of direct and social effects of individuals on feeding behavior traits.

An approach for modeling the social effect on feeding behavior traits analyses is by fitting social genetic effect (SGE) models (Griffing, 1967, 1968a, 1968b; Moore et al., 1997; Muir, 2005; Bijma et al., 2007), whereby it is possible to estimate the direct genetic effect of an individual's genotype on their phenotype and the influence of SGE of the individual on the phenotypic expression of their group mates. A few studies have reported the implementation of SGE models on feeding behavior traits, including daily occupation time, average daily feed intake (AFI), and average daily feeding rate for pig populations (Chen et al., 2010; Herrera Cáceres, 2016; Herrera Cáceres et al., 2019). Some of these studies found a partial confounding effect between SGE and some common environmental effects, due to the use of small datasets and the complexity of SGE models, which for some feeding behavior traits resulted in very large standard errors in the estimated social variance and covariance with direct effects. All these studies summarized the records of the whole feeding testing period into a single record per animal

and proceeded to fit SGE models that assumed an average interaction value for all animals in the same social group.

An alternative modeling approach is to fit social effects of feeding behavior traits in group-housed pigs at the level of single feeding event records. This consists of modeling the record of each feeding event or visit at the feeder during the whole testing period, by using the sequence of visits by pigs in the group at the feeder as a proxy for the social interaction between individuals. The goal of this study was to demonstrate that individual automatic feeder record data can be used to estimate social effects on a feed behavior trait. To achieve this, we fit alternative mixed models to the feeding time (visit length) of group-housed pigs, by conditioning on the sequence of feeder visits and estimating the proportion of social and direct variance that is recovered from alternative models.

Material and Methods

All animal protocols were approved by the Institutional Animal Care and Use Committee (Animal Use Form number 01/17-007-00) of Michigan State University, East Lansing, MI, 48842.

Experimental population and data set

Animals used for this study were housed at the Michigan State University Swine Teaching and Research Center, East Lansing, MI. The dataset consisted of the visit duration time (min) at the automatic feeder from records obtained from April 2018 until December 2019, from 135 crossbred pigs in the grow-finish stage distributed over 14 pens (2 pens per trial, 7 trials; pen dimension: 2.44 × 4.88 m), with a mean initial weight of 34 kg (SD ± 7.29; Figure 1). Pigs were provided ad libitum access to feed and subjected to the same management. Each trial continued for different durations, with 30 d minimum and 75 d maximum, and there were varying numbers of individuals per pen (8 to 12 pigs per pen) in each trial.

Experimental pens had a single-space feed intake recording equipment system (FIRE Osborne Industries, KS, USA) that registered individual feed intake variables for each feeder visit. The sides of the feeder were blocked by boards so that there was only one way to enter and exit the feeder (Figure 1). Records included start and end times of visits, date, feed consumed, animal weight, and animal ID. The data were edited to remove anomalous records. Specifically, data from the first 7 d post-occupation of the pens were deleted to allow for animals to adapt and to learn access to the feeders. Brief feeding events typically less than 2-min long usually resulted in intake not being recorded and/or body weight not being recorded, so those events were also removed. If an animal ended a feeder visit and shortly after reentered the feeder, we did not consider it a "follower" of itself, and we ignored such records. Instead, we only included feeding records where the feeding pig left the feeder and was replaced by another pig. After data editing, a total of 74,413 records were kept for further analysis. For each feeding record, we added the identity of the following pig (i.e., the ID of the pig in the next feeding record) and the time elapsed between the end of the current visit and the start of the next visit (i.e., time to next visit or replacement time for the current visit).

In this study, we assumed that, if there was a social effect on a feeding duration, such an effect came from the pig that replaced the current pig at the feeder (we call that replacement animal the follower or following pig), as long as the replacement occurs in a short period of time. Because the goal of this study was to investigate the effect of the following pig on the time at the feeder of the feeding pig, the data were divided into two subsets

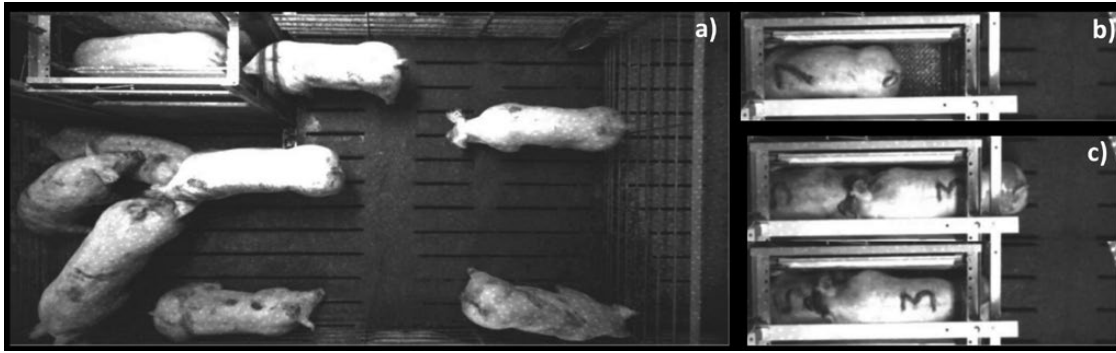


Figure 1. Pen layout and interactions between animals. Panel (a) shows a top-down infrared image view of the overall pen layout with 9 pigs in it. In the upper left corner, a pig is inside the feeding space eating and a following pig is behind it. Panel (b) zooms into the feeder area and shows a single pig eating from the feeder. Panel (c) shows a sequence of two images taken moments apart and it shows a following pig mounting a feeding pig in an attempt to displace it from the feeder. These images were taken in the same pens used for data collection in this paper, but they were part of a different study and they are shown here for illustrations of the experimental setup.

Table 1. Number of individuals, number of individuals per pen, and number of records by each subset of data defined according to replacement time to the next visit at the feeder¹

Item	IRT (≤60 s)	NIRT (≥600 s)	Total records
Number of animals	135	135	135
Number of animals per pen	10 ± 2	10 ± 2	10 ± 2
Number of records	58,255	6,256	74,413
Replacement time	≤ 60 s	≥ 600 s	NA

¹IRT, immediate replacement time: time between successive visits at the feeder < 60s; NIRT, non-immediate replacement time: time between successive visits at the feeder > 600s.

(Table 1). The first subset contained 6,256 records consisting of visits where the follower occupied the feeder at least 600 s after the current pig left the feeder. We consider this a “null” dataset, where there should be no effect of the following pig on the meal duration of the currently feeding pig and we called this event a “non-immediate replacement” time (NIRT). The second subset contained 58,255 records, where the time elapsed between the end of the current visit and the start of the next visit was less than or equal to 60 s. We assume that when one pig replaces another in such a short amount of time, the effect of the following pig on the currently eating pig will be manifested if it exists (Figure 1), and we called this data “immediate replacement” time (IRT). We acknowledge that this division of data is arbitrary, and we will discuss alternative partitions later in this paper.

Statistical models and data analysis

Three mixed models were used to model visit duration (time at the feeder). First, we fit a model that ignores the follower and that only models visit duration as a function of fixed effects plus the random effect of the feeding pig (equation 1):

$$y = X\beta + Z_d a_d + e \quad (1)$$

The $n \times 1$ vector y contains duration of visit (in min), and X is the $n \times p$ incidence matrix relating the records to the vector of fixed effects β of order p , which included the contemporary group, hour of entry to the feeder, and the median weight of the pig as a covariate. Matrix Z_d of order $n \times q$ ($q = 135$, i.e., the number of animals) relates records in y to the random vector of animal effects a_d ($q \times 1$), the distribution of the animal effects was

assumed to be $a_d \sim N(0, I\sigma_a^2)$, where I is the Identity matrix, σ_a^2 is the animal variance, e ($n \times 1$) is the vector of random errors that is distributed as $N(0, I\sigma_e^2)$, and σ_e^2 is the error variance; both sets of random effects were assumed to be independent. Because of the lack of genetic information (such as pedigree or genomic markers), the analysis was limited to phenotypic animal effects. Identifiability for the individual effects was then attained due to repeated data on the same animal. The variance proportion explained by the animal effect ($Prp \hat{\sigma}_a^2$) for the model in equation 1 was estimated as the ratio between the animal variance (σ_a^2) and total phenotypic variance (σ_p^2):

$$Prp \hat{\sigma}_a^2 = \frac{\sigma_a^2}{\sigma_p^2} = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2} \quad (2)$$

Where $\hat{\sigma}_a^2$ and $\hat{\sigma}_e^2$ are the estimated variance components for the direct variance and error variance, respectively.

A second model was fit to include the social effect, hereby named the “follower effect” to indicate the effect of the animal replacing (following) the current (feeding) pig at the feeder. The full model is represented below:

$$y = X\beta + Z_d a_d + Z_f a_f + e \quad (3)$$

Fixed, genetic direct, and error random effects were the same as in equation 1. Here Z_f denotes the incidence matrix associating the random vector effects of follower additive effects a_f ($q \times 1$) to the data in y . The distribution of follower additive effects was assumed to be $a_f \sim N(0, I\sigma_f^2)$, with σ_f^2 being the additive follower variance.

The third model fitted had a model equation identical to equation 3, except for the inclusion of a covariance structure between direct and follower random effects, which was specified by the sigma matrix Σ :

$$\Sigma = \begin{bmatrix} \sigma_a^2 & \rho\sigma_a\sigma_f \\ \rho\sigma_a\sigma_f & \sigma_f^2 \end{bmatrix}$$

The scalar ρ represents the within animal correlation between direct and follower random effects. For the models fitted with equation 3, the variance proportion explained by the direct effect ($Prp \hat{\sigma}_a^2$) and variance proportion explained by the follower effect ($Prp \hat{\sigma}_f^2$) were estimated in the same way as equation 2, but the $\hat{\sigma}_p^2$ was estimated including the follower

variance estimate ($\hat{\sigma}_f^2$) and two times the covariance ($2\hat{\rho}\hat{\sigma}_d\hat{\sigma}_f$). Bayesian procedures were used to estimate (co)variance parameters plus the fixed effects in β . Flat priors were assumed for $\beta \sim U(-\infty, +\infty)$, for the variance components σ_a^2 , $\sigma_f^2 \sim U(0, 100)$, for the error variance $\sigma_e^2 \sim U(0, \infty)$, and for the ρ parameter $U(-1, 1)$.

Estimation of (co)variance components

For all statistical analyses, the marginal posterior distribution of all unknown parameters was obtained by Markov chain Monte Carlo (MCMC) sampling, through the No-U-Turn sampler variant of Hamiltonian Monte Carlo algorithm implemented in the Stan program (Carpenter et al., 2017), which is available through a variety of interfaces such as RStan in R. Three chains of 12,000 samples were run in parallel, and the first 2,000 iterations by chain were discarded. As the thinning interval was 1, 30,000 samples were left to assess the convergence and to obtain posterior estimates of the parameters.

Convergence diagnostics

To determine convergence of the Markov's chains to a common stationary distribution, we employed Gelman and Rubin's diagnostic (Gelman and Rubin, 1992; Gelman et al., 2013) and Geweke's (1991) convergence criteria. Additionally, we computed autocorrelation coefficients, effective sample size, and Monte Carlo standard errors for all chains. In order to discard convergence problems, all diagnostic tests were calculated using the functions available in rstan, coda, bayesplot, and mcmcplots packages from R. A summary of the convergence diagnostics is presented in [Supplementary Appendices 1–3](#).

Model comparison

Competing models predictive accuracy was assessed through Bayesian model comparison with the Watanabe–Akaike widely available information criterion (WAIC; Watanabe, 2010), which is a Bayesian approach for estimating the expected log pointwise predictive density (elpd) (Gelman et al., 2013; Vehtari et al., 2016). The WAIC for each model was calculated using functions in the loo package of R. To compare the predicting performance of a pair of models, the difference in their $-2 \times \text{elpd}$ and its standard error was computed. Although there is no “hard and fast rule,” the difference between alternative statistics should be greater than the variation due to Monte–Carlo sampling (Vehtari et al., 2016; Whalen and Hoppitt, 2016).

Estimating Best Linear Unbiased Predictor of feeder visit duration time

For reasons of computational expediency, we did not save MCMC output on random animal effects from our Bayesian model fit procedure. Consequently, to obtain a quick prediction of social and direct effects through the Best Linear Unbiased Predictor (BLUP Henderson; Henderson, 1975), we used Restricted Maximum Likelihood (Patterson and Thompson, 1971), by refitting the selected model (equation 2) to an IRT dataset ($N=58,255$ records). Function lmer from package lme4 in R was used for this purpose.

Correlation between BLUP of direct and follower effects on visit duration time at the feeder and other traits

To investigate the relation between the predicted effects of feeding pig (direct) and follower pig (indirect social effects)

to other feeding behavior and growth traits, we calculated Pearson's correlation coefficients.

Weight gain

The weight gain (WG) for each individual pig was analyzed using 74,413 records with a random regression model. Using median daily weight on each trial as a covariate, the model equation (in scalar notation) was as follows:

$$y_{ikj} = \beta_{0k} + \beta_{1k}x_{ij} + u_{0i} + u_{1i}x_{ij} + e_{ikj} \quad (4)$$

The data y_{ikj} are the median weight for the i th animal from the k th group taken on the j th test day, β_{0k} and β_{1k} are the fixed, group-specific, intercept and slope, respectively, u_{0i} is the animal random effect, u_{1i} is the random slope over time for each animal, x_{ij} is the corresponding test day (days in test), and e_{ikj} is the random error, which is independent of u_{0i} and u_{1i} . We assumed the distribution of random effects as following, $u_{0i} \sim N(0, \sigma_{u_0}^2)$, $u_{1i} \sim N(0, \sigma_{u_1}^2)$, $e_{ikj} \sim N(0, \sigma_e^2)$, whereas the covariance structure between u_{0i} and u_{1i} is equal to:

$$\text{Cov} \begin{bmatrix} u_0 \\ u_1 \end{bmatrix} = \begin{bmatrix} \sigma_{u_0}^2 & \sigma_{u_0u_1} \\ \sigma_{u_0u_1} & \sigma_{u_1}^2 \end{bmatrix}$$

The scalar $\sigma_{u_0u_1}$ is the covariance between animal and random slope effects. The group-corrected WG estimated for the i th pig was calculated as $\widehat{WG}_i = \hat{u}_{1i}$.

Feed intake

Raw AFI was calculated as the ratio between the total feed consumed (kg) by an individual and the total number of trial days with 74,413 records of consumption from the automatic feeders. The AFI was corrected by a fixed effects linear model to account for trial differences as follows:

$$y_{ij} = \mu_j + e_{ij} \quad (5)$$

The observation y_{ij} is the AFI of i th individual in the j th group, μ_j is the contemporary group mean, e_{ij} is the random error for each individual in each group, and $\hat{e}_{ij} = y_{ij} - \hat{\mu}_j$ is the deviation for the AFI of the i th animal with respect to the estimated group mean.

Daily feeder occupation time

The average time per day spent eating for each animal was analyzed as the ratio between the sum of the total time of feeder occupation (in min) for each individual and the total number of trial days corrected by the group mean, and the statistical model was equal to:

$$y_{ij} = \mu_j + e_{ij} \quad (6)$$

The observation y_{ij} is the average of feeder occupation (minutes) from the i th pig in the j th group, μ_j is the contemporary group mean, e_{ij} is the random error for each individual in each group, and $\hat{e}_{ij} = y_{ij} - \hat{\mu}_j$ is the daily feeder occupation time (FOT) as deviation of the i th animal with respect to the estimated group mean.

Results and Discussion

Estimation of (co)variance components for feeder visit duration

Means and quantiles of the posterior distributions of the variance components for visit duration in each dataset, and for

each of the three models of analysis, are presented in Table 2. For the subset of data where the replacement of feeding animals was immediate (IRT), that is, when the time between the end of a visit and the start of the next visit was less than or equal to 60 s, the posterior mean of the proportion of variance explained by the feeding animal effect ($Prp \hat{\sigma}_a^2$) was approximately 18%, regardless of model fit, while the proportion of variance explained by the follower social effect ($Prp \hat{\sigma}_f^2$) was approximately 2%, for the estimates from both models 2 (M2) and 3 (M3), respectively. On the contrary, with non-immediate visits (NIRT), the variance component associated with the follower effect was almost zero, while $Prp \hat{\sigma}_a^2$ was close to 20%. The estimated posterior mean of the correlation between direct (feeding pig) and social (following pig) effects under M3, using the IRT data set, was $\hat{\rho} = 0.12$ and the posterior quantiles for $\hat{\rho}$ at the 2.5% and 97.5% percentiles were -0.069 and 0.307 , respectively. On the other hand, for the NIRT data set, the posterior mean for $\hat{\rho}$ and the posterior quantiles at 2.5% and 97.5% were, -0.90 and 0.78 , respectively. Such a wide dispersion in the posterior distribution of a correlation parameter leading to high uncertainty about the sign of the correlation is a hint for uncorrelated direct and social effects. Thus, we performed a model comparison to formally test for the value of the correlation between social and direct animal effects (see Results below).

The posterior mean of the residual variance ($\hat{\sigma}_e^2$) for the data on feeding records with IRT was 43.05 for M1 and 41.90 in M2 and M3. Notice that the decrease in residual variance when adding the follower effect (M1 vs. M2) is equal to the variance of the follower effect, which suggests that there is not confounding between the animal and the follower effects. This result is in agreement with the model comparison, as the estimated values of the WAIC (Table 3) display a better fit for M2 over M1. The difference between these models in the expected log of the pointwise predictive density ($elpd$) was equal to -731.1 ($SE = 41$). Furthermore, when the covariance between animal and the follower effects was included in M3, there was no improvement in model fit over the one observed in M2. Therefore, the estimate of the difference in $elpd$ among M2 and M3 was equal to -0.1

($SE = 0.5$). On the other hand, in the case of feeding records with NIRT, the posterior distribution of $\hat{\sigma}_e^2$ was virtually identical for the three models (Table 2), which reflects that there were no effects of the follower on the duration of the current animal's visit at the feeder. This is reinforced by the fact that the values of the WAIC were similar for the three models (Table 3), which in turn induced a difference in $elpd$ between M1 and M2 of -1.35 ($SE = 0.64$) and between M1 and M3 of -1.35 ($SE = 0.59$).

In other research with group-housed pigs (Hall, 1997; Labroue et al., 1997; Hall et al., 1999; Chen et al., 2010; Herrera Cáceres, 2016; Lu et al., 2017; Herrera Cáceres et al., 2019), the time of visit to the automatic feeder has been calculated as the sum of the total occupation time in the testing period divided by the number of days in the testing period. These researchers estimated variance components and genetic parameters employing an animal model similar to M1 (see equation 1). For example, using small data sets ($547 < N < 1,832$) with records of time at the feeder, Hall (1997) and Hall et al. (1999) estimated $Prp \hat{\sigma}_a^2$ of an order 8% of the phenotypic variance, whereas Chen et al. (2010), Herrera Cáceres (2016), and Herrera Cáceres et al. (2019) estimated that the proportion of variance of the animal effect was equal to 38%, 39%, and 23%, respectively. In contrast, Lu et al. (2017) and Labroue et al. (1997) used larger data sets ($3710 < N < 14901$) and estimated $Prp \hat{\sigma}_a^2$ at 71% and 40% of the phenotypic variance. Although, in the current study, the visit duration of each animal uses every recorded event in the automatic feeder from two different replacement times (immediate or non-immediate), our estimates of $Prp \hat{\sigma}_a^2$ are within the range reported by the authors mentioned above.

A distinctive feature of our proposed analysis is to simultaneously assess the direct effect of the current animal that is eating and the indirect or social effects of the animal that follows the eating pig. In doing that, we used the sequence of visits at the feeder to apportion the social effects of each animal to the immediate follower by fitting M2 and M3. Our models are inspired by SGE models (Cantet and Cappa, 2008; Cappa and Cantet, 2008; Bijma, 2010) in the sense that we fit direct (feeding pig) and social (following pig) effects. However, we did not have

Table 2. Posterior statistics for each variance component and variance proportion explained on visit duration time at the feeder with two different replacement times and three mixed models

Model	Parameter ¹	IRT (<=60 s)				NIRT (>=600 s)			
		Mean	q 2.5%	q 50%	q 97.5%	Mean	q 2.5%	q 50%	q 97.5%
M1	$\hat{\sigma}_a^2$	9.664	7.458	9.555	12.530	11.51	8.515	11.34	15.41
	$\hat{\sigma}_e^2$	43.050	42.560	43.05	43.54	43.50	41.99	43.49	45.07
	$Prp \hat{\sigma}_a^2$	0.182	0.147	0.181	0.225	0.208	0.163	0.206	0.262
	$Prp \hat{\sigma}_e^2$	0.817	0.774	0.818	0.852	0.791	0.737	0.793	0.836
M2	$\hat{\sigma}_a^2$	9.591	7.397	9.472	12.43	11.49	8.48	11.34	15.34
	$\hat{\sigma}_f^2$	1.297	0.983	1.280	1.710	0.065	0.001	0.040	0.261
	$\hat{\sigma}_e^2$	41.90	41.43	41.90	42.37	43.47	41.93	43.46	45.10
	$Prp \hat{\sigma}_a^2$	0.181	0.146	0.179	0.223	0.208	0.162	0.206	0.261
M3	$Prp \hat{\sigma}_f^2$	0.024	0.018	0.024	0.033	0.0011	0.00002	0.00074	0.0047
	$Prp \hat{\sigma}_e^2$	0.794	0.752	0.795	0.828	0.790	0.737	0.792	0.836
	$\hat{\sigma}_a^2$	9.697	7.468	9.584	12.62	11.53	8.548	11.37	15.39
	$\hat{\sigma}_f^2$	1.312	0.989	1.297	1.723	0.064	0.010	0.043	0.231
M3	$\hat{\rho}$	0.121	-0.069	0.122	0.307	-0.103	-0.903	-0.113	0.787
	$\hat{\sigma}_e^2$	41.90	41.42	41.90	42.38	43.47	41.95	43.46	45.06
	$Prp \hat{\sigma}_a^2$	0.182	0.147	0.181	0.226	0.208	0.163	0.207	0.261
	$Prp \hat{\sigma}_f^2$	0.0248	0.018	0.024	0.032	0.0011	0.00019	0.0007	0.0042
M3	$Prp \hat{\sigma}_e^2$	0.792	0.750	0.793	0.827	0.790	0.731	0.791	0.834

¹ $\hat{\sigma}_a^2$, direct genetic variance; $\hat{\sigma}_f^2$, follower variance; $\hat{\sigma}_e^2$, error variance; $\hat{\rho}$, correlation between direct and follower effects; Prp , variance proportion explained by each variance component; q , quantiles of the distribution.

Table 3. Model comparison through the WAIC on visit duration time at the feeder with two different replacement times

Model	IRT (≤ 60 s)			NIRT (≥ 600 s)		
	elpd ¹	p _{waic}	WAIC	elpd	p _{waic}	WAIC
MM1	-192,339.2	181.7	384,678.4	-20,763.44	166.78	41,526.88
M2	-191,608.1	301.1	383,216.3	-20,764.91	173.81	41,529.81
M3	-191,608.3	301.3	383,216.6	-20,764.79	172.76	41,529.59

¹elpd, expected log pointwise predictive density; p_{waic}, effective number of parameters.

information on additive relationships among animals; thus, we had to limit our analysis and conclusion to phenotypic direct and social effects. However, the most salient feature of the proposed analysis compared, with other social effects models, is that, while in traditional social effects models (Bijma et al., 2007), there is typically a single observation per animal and a single element in the incidence matrix linking the phenotypic value of an animal to the social effects of all group mates; in our model, each observation from an animal is linked to the social effect of a single animal in the same pen. Moreover, single feeder visit data collected from pigs from their entire finishing phase resulted in all possible combinations of feeding and following pigs in each social group, which helped in separating direct from follower effects in M2 and M3. Specifically, we did not have to apportion the social effect of a phenotypic observation in equal parts to all group mates; instead, we just apportioned the social effect of a particular observation to the animal immediately following the current pig in the feeding records. This allowed us to separate social variance from direct variance as we report below.

We found that the proportion of phenotypic variance explained by the social effect ($P_{rp} \hat{\sigma}_p^2 = 2\%$) was small but significantly different from zero, as long as we focused on feeding records where the time to the next visit was less than or equal to 1 min. There are few investigations on the estimation of direct and indirect genetic effects on feeding behavioral traits of pigs. Initial results were from Chen et al. (2010) and Herrera Cáceres (2016), who fitted a classical model with SGE (IGE; Bijma et al., 2007) to estimate both the direct and indirect genetic effects for daily occupation time at the feeder. Chen et al. (2010) worked with a small data set and employed a complex model including indirect genetic effects (IGE). As a consequence, their estimated variance components exhibited large SEs. Similarly, Herrera Cáceres (2016) estimated a value of 61% for the proportion of variance of the social effect, though the SE was also large: 40% of the absolute value of the parameter.

The resulting estimates from M3 (Table 2) suggest that there is no correlation between random additive effects of the feeding animal and its follower effect, contrary to the results obtained by Herrera Cáceres (2016) and Herrera Cáceres et al. (2019). These authors fitted the IGE model to estimate the genetic correlation between direct effect and indirect effect for the daily occupation time at the feeder and estimated correlations of -0.83 and -0.78, respectively. An important difference between our way of modeling social effects and the one used by Herrera Cáceres (2016) and Herrera Cáceres et al. (2019) is that, as we explained above, we modeled each feeding record individually and attributed the indirect effect only to the following pig, whereas Herrera Cáceres (2016) and Herrera Cáceres et al. (2019) used a classic social effect model that apportions

competition or social effects equally to all pen mates. Moreover, while classic social effects models focus on modeling SGE, our modeling focused on phenotypic social effects, as we did not include a relationship matrix due to the lack of pedigree information in the commercial system from which measures were taken.

As mentioned above, the replacement time chosen to partition the data into the null dataset (NIRTs) and the dataset with competition for feeding space (IRTs) was arbitrary. However, to study the influence of the proposed splitting thresholds in the estimated parameters, we performed a sensitivity analysis by splitting the dataset into eight different subsets of data by using different thresholds and refitting M1 (equation 1) and M2 (equation 3). We found that any replacement threshold between 30 and 60 s resulted in virtually identical estimated variance components compared with the IRT data set (see Supplementary Appendix 4). Similarly, any replacement threshold above 90 s generated a null dataset similar to the NIRT dataset, and the estimated variance components were virtually identical to those presented in the current paper. Our choice of splitting thresholds for the replacement times attempted to have a good balance between the number of records and the ability to assess our assumption. Specifically, we assumed that when the follower quickly replaces the feeding pig in the feeder (IRT), the effect of the follower (social effect of competition) will manifest itself by a shorter feeding time of the current pig at the feeder, depending on the competition ability of the following pig. On the other hand, when the follower enters the feeder long after the current feeding pig has left (NIRT), the social effect of the follower will not be expressed in the meal duration of the current feeding pig.

A potential criticism of our approach to detect following animals is the fact that the follower might not have caused the displacement of the currently eating animal from the feeder (competition for feeding space) but another pig may have caused the displacement, and the observed follower just entered the feeder as soon as it was vacated. We cannot confirm or discard this possibility because of the lack of behavioral observations. However, the fact that an animal is able to quickly occupy a vacated feeder is an indication of a high competition ability even when there are other pigs displacing the feeding animal. Thus, if the time at the feeder for any pig is shortened when compared with the average feeding time of that animal, the competition effect will be apportioned to the following pig in our model. Further confirmation of this requires behavioral observations of displacement at the feeder and feeder occupation.

The results from this study in grow-finish pigs showed that modeling each recorded visit to the automatic feeder resulted in a social phenotypic variance (or follower variance component) of about 13% of the direct variance. Considering the indirect effect of the follower on the meal duration of feeding pigs, the proportion of variance explained by the social effect was small, although we recovered more residual variability than when only the direct effect was included in the model. The differences in the results obtained with respect to other research carried out in feeding behavior using automatic feeders may be related to the way the recorded trait is defined and to the influence of environmental factors, such as space, density, and group size (Nielsen et al., 1995; Hoy et al., 2012; Hyun and Ellis, 2002), which in our research may have allowed pigs to have equal opportunity to access the feeder.

Phenotypic correlation of BLUP of direct and social effects for the duration of visits at the feeder and other phenotypes

The predicted BLUP of direct and social random effects in the model in equation 3 with data from IRT was correlated with WG, AFI, and daily FOT. The estimated Pearson correlation coefficients (\hat{r}) between pairs of traits and their associated P-values are displayed in Table 4. The data on WG and AFI for an individual were not significantly correlated with its own predicted direct effect on the visit duration at the feeder (Direct BLUP); likewise, the predicted follower effect on visit duration at the feeder of an animal (Follower BLUP) was also uncorrelated with the WG and AFI estimates of its group mates. In the case of the average time the individual spent eating or FOT, the estimated value was high and significant ($\hat{r} = 0.51$) with the predicted Direct BLUP and moderately negative ($\hat{r} = -0.26$) with predicted Follower BLUP for visit time at the feeder.

Other researchers have estimated direct genetic correlations between daily occupation time and average daily gain ranging from 0.11 to 0.46 and for daily occupation time and average feed intake from 0.14 to 0.35 (Hall, 1997; Labroue et al., 1997; Hall et al., 1999; Herrera Cáceres, 2016; Lu et al., 2017). However, Herrera Cáceres et al. (2019) found no genetic correlation between those traits, and Chen et al. (2010) also estimated a nonsignificant correlation ($\hat{r} = 0.04$) between predicted direct breeding values of daily occupation time and average daily gain. However, this last set of estimates is in agreement with our value ($\hat{r} = 0.09$) for the correlation between WG and Direct BLUP for visit length time at the feeder. In addition, Chen et al. (2010) found a significant \hat{r} (0.33) between predicted direct breeding values of daily occupation time and AFI, a value that was estimated by us to be $\hat{r} = 0.09$. Moreover, the studies by Herrera Cáceres (2016) and Herrera Cáceres et al. (2019) fitting bivariate models with IGE have reported estimates of genetic correlations between direct and indirect effects of the same order of magnitude as their SEs.

The visit duration consists of the length of a specific feeding event, whereas the daily FOT condenses the information of the daily records of feeder occupation, to describe the amount of time (in min) that an animal spent at the feeder per day. We expected that in the current study the correlation between Direct BLUP of visit duration at the feeder and FOT would be positive, which is what we observed ($\hat{r} = 0.51$, $P < 0.05$). Moreover, it is interesting to observe that predicted Follower BLUP for visit duration and FOT showed a significantly negative correlation ($\hat{r} = -0.26$, $P < 0.05$). This result indicates that animals that spend more time per day at the feeder (larger FOT) caused other animals to have shorter meals, that is, the Follower BLUP decreases.

Table 4. Pearson correlation coefficient between direct and follower BLUPs of visit duration time at the feeder and other traits and their P-values in pig production

Trait	Direct BLUP		Follower BLUP	
	\hat{r}^1	P-value	\hat{r}	P-value
WG	0.0956	0.269	-0.0018	0.983
AFI	0.0932	0.282	0.0054	0.950
FOT	0.5061	0.000*	-0.258	0.002*

¹ \hat{r} , estimate Pearson correlation coefficient.

* $P < 0.05$.

Conclusions

In summary, the length of visits in automatic feeders in this study was subject to significant direct (feeding pig) and social (follower) effects when the replacement time between visits was short (<1 min). In addition, animals that had larger FOT shortened the meal length of the preceding individuals at the feeder. This effect was clearly evident in our study due to the presence of a single feeder space. Further studies in multi-space feeders while incorporating behavioral observations are warranted to confirm these effects. Our proposed modeling approach can be used with automatic feeding records and could easily be expanded to incorporate genetic effects and direct behavioral observations.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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Conflict of interest statement

The authors declare no conflict of interest.

Data availability

All data and code necessary for reproducing the results of this study are publicly available in github at: https://github.com/belcyangarita/Github_Visit_Duration.

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