

# Genetic parameter estimation and evaluation of Duroc boars for feed efficiency and component traits

M. D. MacNeil<sup>1</sup> and R. A. Kemp<sup>2</sup>

<sup>1</sup>Delta G, 145 Ice Cave Rd., Miles City, Montana 59301, USA and Animal and Grassland Sciences, University of the Free State, Bloemfontein 9300, South Africa; and <sup>2</sup>RAK Genetic Consulting Ltd., 54 Coachwood Point W, Lethbridge, Alberta, Canada T1K 6A9.

Received 11 June 2014, accepted 16 December 2014. Published on the web 19 December 2014.

MacNeil, M. D. and Kemp, R. A. 2015. **Genetic parameter estimation and evaluation of Duroc boars for feed efficiency and component traits.** *Can. J. Anim. Sci.* **95**: 155–159. The objective of this research was to produce a genetic evaluation for traits related to feed efficiency of Duroc boars. Meeting this objective required partitioning phenotypic (co)variance into additive genetic and environmental components for feed intake and traits indicative of growth and body composition. Boars ( $N = 3291$ ) were housed in group pens of 22 to 24 animals with two electronic feeders per pen and feed intake was recorded for 8 to 14 wk. Body weight was recorded for each boar at the start and end of test, at approximately 100 kg and at up to three times during the test. The pedigree used contained sire and dam of each boar with at least one recorded phenotype ( $N = 4651$ ) and their maternal and paternal grandsires. Variance components were estimated by restricted maximum likelihood for animal models in a series of uni-variate and bi-variate analyses. Two multiple trait genetic evaluations were conducted to predict estimated breeding value for feed intake using animal models. The first evaluation included feed intake ( $h^2 = 0.33 \pm 0.05$ ), age at 100 kg ( $h^2 = 0.31 \pm 0.04$ ), and subcutaneous fat depth ( $h^2 = 0.47 \pm 0.05$ ). The second genetic evaluation included feed intake, average daily gain ( $h^2 = 0.27 \pm 0.04$ ), mid-test weight ( $h^2 = 0.33 \pm 0.05$ ), and subcutaneous fat depth. Genetic correlations of feed intake with age at 100 kg and fat depth were  $-0.80 \pm 0.05$  and  $0.57 \pm 0.08$ , respectively. Estimated breeding values for measures of feed efficiency (residual feed intake and residual gain) were calculated from the results of the second analysis and the associated additive genetic (co)variance components.

**Key words:** Feed efficiency, production, swine, variance components

MacNeil, M. D. et Kemp, R. A. 2015. **Estimation des paramètres génétiques et évaluation des verrats Duroc pour l'efficacité alimentaire et les paramètres de ses composants.** *Can. J. Anim. Sci.* **95**: 155–159. L'objectif de cette recherche était de produire une évaluation génétique des paramètres reliés à l'efficacité alimentaire des verrats Duroc. Répondre à cet objectif nécessitait la répartition de la (co)variance phénotypique en composants génétiques et environnementaux additionnables pour la prise alimentaire et les caractéristiques indicatrices de croissance et de composition du corps. Les verrats ( $N = 3291$ ) ont été logés dans des enclos en groupes de 22 à 24 animaux, deux dispositifs électroniques d'alimentation par enclos et la prise alimentaire était enregistré pendant 8 à 14 semaines. Le poids corporel était noté pour chaque verrat au début et à la fin de chaque test, autour de 100 kg et jusqu'à trois fois pendant chaque test. Le pedigree utilisé contenait l'information sur le père et la mère avec au moins un phénotype enregistré ( $N = 4651$ ) et sur les grands-pères maternels et paternels de chaque verrat. Les composants de variance ont été estimés par le maximum restreint de vraisemblance des modèles animaux dans une série d'analyses unidimensionnelles ou bidimensionnelles. Deux évaluations de caractéristiques génétiques multiples ont été effectuées pour prédire les valeurs d'élevage espérées (EBV – « estimated breeding value ») pour la prise alimentaire utilisant des modèles animaux. La première évaluation comprenait la prise alimentaire ( $h^2 = 0,33 \pm 0,05$ ), âge à 100 kg ( $h^2 = 0,31 \pm 0,04$ ), et la profondeur du gras sous-cutané ( $h^2 = 0,47 \pm 0,05$ ). La deuxième évaluation génétique comprenait la prise alimentaire, le gain moyen quotidien ( $h^2 = 0,27 \pm 0,04$ ), poids au mi-test ( $h^2 = 0,33 \pm 0,05$ ), et la profondeur du gras sous-cutané. Les corrélations génétiques de la prise alimentaire avec l'âge à 100 kg et la profondeur du gras étaient de  $-0,80 \pm 0,05$  et  $0,57 \pm 0,08$ , respectivement. Les EBV pour les mesures d'efficacité alimentaire (prise alimentaire résiduelle et gain résiduel) ont été calculés à partir des résultats de la deuxième analyse et les composants de (co)variance génétique additionnables associés.

**Mots clés:** Efficacité alimentaire, production, porcs, composants de variance

It has long been recognized that differences among animals in conversion of feed into body weight is an important determinant of profit from pork production. Feed efficiency is not a directly measurable trait, but must be calculated from component traits (Koch et al. 1963). Further, the linear combination of feed intake and growth to calculate a feed efficiency metric does provide new information relative to that which is obtainable from the component traits (Kennedy et al. 1993).

The greatest efficacy in genetic improvement of production efficiency requires simultaneous consideration of estimated breeding value (EBV) for both inputs (e.g., feed)

**Abbreviations:** ADG, average daily gain; D100, age at 100 kg live weight; EBV, estimated breeding value; FAT, subcutaneous fat depth, FI, feed intake; LMD, longissimus muscle depth; RFI, residual feed intake; RG, residual gain; RIH, correlation of predicted and true breeding values or accuracy of EBVWT, mid-test weight

and outputs (e.g., body weight). Additionally, indexes combining inputs and outputs, such as residual feed intake and residual gain (Koch et al. 1963) may enhance communication of differences in efficiency among animals. Objectives of this research were to produce a genetic evaluation for feed intake and additional traits related to the feed efficiency of Duroc boars and provide required parameters to facilitate incorporation of cost of feed consumed into economic selection indexes.

### MATERIALS AND METHODS

Data were collected at the Daly Research and Development Facility (CanAm Genetics, Oakville, MB). Feed intake, body weights, and ultrasonic depths of subcutaneous fat and loin muscle were obtained for boars reared under commercial production-like conditions. Boars were fed one pelleted diet from 25 to 120 kg offered to appetite. The diet was composed of wheat, peas, soybean meal, canola meal, amino acids, vitamins and minerals. Diet was formulated to 2.40 Mcal of net energy and 1.0% standard ileal digestible lysine, with other amino acids set relative to lysine on a standard ileal digestible basis to exceed the pigs requirements. All animals were cared for in accordance with guidelines established by the Agriculture and Agri-Food Canada (Conner 1993).

Daily feed intake was recorded for a total 4841 Duroc boars between 2004 May 06 and 2010 Dec. 31. Boars were sampled from the purebred Duroc population housed at the research and development facility. The sampling procedures were to have, on average, two boars from each litter (approximately 12 litters born per week) identified for the feed intake test on a weekly basis. At weaning (approximately 21 d of age), test boars were grouped into a single pen during the nursery phase. At completion of the nursery phase (approximately 9 wk of age) each group of boars was put into a single test pen ( $n = 22$  to 24 boars per pen) fitted with two electronic feeders per pen (IVOG, Insentec BV, Marknesse, the Netherlands). Following a 7-d acclimation period each boar received a radio frequency identification ear tag and start of test weight was recorded. The test length was 14 wk with individual weights taken at the end of test and approximately every 3 wk during the test period. Additionally when the pen average weight was near 100 kg, boars were individually weighed and depths of subcutaneous fat and longissimus muscle were measured over the last three ribs using ultrasound (Aloka 500, Imagomedical Inc., QC).

Individual meal events were edited to remove outliers and obvious errors using adapted procedures recommended by Casey et al. (2005). Individual meal events outside of the on-test and off-test weights were removed, as were meal events of  $<0.05$  kg and  $>0.35$  kg. Feeding events  $<0.5$  min and  $>$  than 8.0 min were discarded as were feeding events with a rate of consumption  $<0.02$  kg  $\text{min}^{-1}$  and  $>0.10$  kg  $\text{min}^{-1}$ . Boars with fewer than five feeding events per day and more than 30 feeding events per day had all of their feed events removed for that given day.

Following these edits, individual feeding events were aggregated to daily feed intakes for each individual. Length of the period during which feed intake data were collected ranged from 1 to 163 d. Preliminary analyses established the mean and variance of feed intake were approximately equal for test periods of 8 to 14 wk in duration. Thus, records from shorter and longer test periods were deleted from the data as were records that departed from the overall mean by more than three standard deviations.

Data from any boar that did not have a start and end of test weight plus at least one other weight (not including the weight at ultrasound scanning) were discarded. Average daily gain was calculated as linear regression of weight on age using all available weights, mid-test weight (WT) was the average of initial (mean = 31.0 kg, SD = 7.9 kg) and final weights (mean = 112.9 kg, SD = 13.6 kg). At ultrasound measurement, averages of age and weight of the pigs were 154 d (SD = 9 d) and 104 kg (SD = 12 kg), respectively. The age at which each boar weighed 100 kg was calculated from age and weight at ultrasonic scanning and its average daily gain (ADG). Like feed intake (FI), the ADG, WT, age at 100 kg live weight (D100), subcutaneous fat depth (FAT) and LMD phenotypes were edited to remove observations that were more than 3 standard deviations removed from their respective mean. Following these edits, the data were examined to determine normality of the resulting phenotypic distributions. For all traits, estimates of skewness and kurtosis were small.

Variance components were estimated in a series of uni-variate and bi-variate analyses using MTDFREML (Boldman et al. 1993). Contemporary groups were defined by the pen in which the pig resided during the evaluation period and the date of ultrasonic scanning. The magnitude of random permanent environmental effects due to litters was explored in preliminary analyses with models that were otherwise similar to those described below. For all traits except D100, the litter effects were found to explain less than 3% of the phenotypic variation and were thus ignored in further final analyses for the other traits. First the additive genetic and residual components of variance for each trait were estimated with uni-variate models that included fixed contemporary group effects and, except for FI and D100, the linear effect of age at ultrasonic scanning. Convergence of the simplex was assumed when its variance was less than  $d^{-12}$ . For each analysis, convergence was confirmed with an independent analysis from different starting values. Upon completion of the uni-variate analyses to estimate the variance components, bi-variate analyses were conducted to estimate the covariance components. These analyses corresponded to the uni-variate analyses described above with the data that was used restricted to those records from animals with both traits recorded. The bi-variate models also included additive genetic and residual covariance components. Initial estimates of the variance components were those estimated in the

uni-variate analyses and these were held constant during iteration to estimate the covariance components. Again, convergence of the simplex was assumed when its variance was less than  $d^{-12}$  and was confirmed with an independent analysis from different starting values. Following Dodenhoff et al. (1998), standard errors for estimates of the genetic parameters were calculated based on the average information matrix (Johnson and Thompson 1995).

Subsequent to estimation of (co)variance components, two multiple trait genetic evaluations were conducted using BLUP for animal models (Henderson and Quaas 1976). The (co)variance components estimated as described above were assumed to be the population parameters. The first evaluation included FI, D100, and FAT as a prototype genetic evaluation for FI. To produce an evaluation of efficiency measured as either residual feed intake (RFI) or residual gain (RG), a second four-trait BLUP analysis of FI, ADG, WT, and FAT was also conducted. Both evaluations used the estimated variances and covariances as parameter values and fixed effects were included in the model for each trait as described above. Following prediction of breeding values, EBV for RFI and RG were calculated as linear functions of the primary results. Appropriate regression coefficients were calculated simultaneously from the genetic (co)variance estimates. Thus:

$$\begin{aligned} EBV_{RFI} &= EBV_{FI} - 0.8601*EBV_{ADG} \\ &\quad - 0.0155*EBV_{WT} - 0.0252*EBV_{FAT}; \text{ and} \\ EBV_{RG} &= EBV_{ADG} - 0.2567*EBV_{FI} \\ &\quad - 0.0033*EBV_{FAT} \end{aligned}$$

Estimates of additive genetic variance for  $EBV_{RFI}$  and  $EBV_{RG}$  were calculated as variances of the respective linear functions. Finally, estimates of covariance of FI, ADG, WT, FAT and LMA with RFI and RG were calculated as weighted sums of the individual trait covariances. Throughout, the (co)variance components estimated as described above were assumed to be the population parameters.

## RESULTS AND DISCUSSION

The data contained progeny of 223 sires, 162 of which had offspring with records of FI. Fifty of these sires also had a recorded FI. Considering all pigs with at least

one recorded phenotype, the average number of progeny per sire was 20.0. When only those pigs with recorded FI were counted, the average number of progeny per sire was 20.3. Likewise, there were progeny of 1146 dams in the data, with 878 of the dams having offspring with records of FI. Considering all pigs that contributed to the data, the average number of progeny per dam was 4.1. The average number of progeny per dam was 3.7, when only those pigs with recorded FI were counted.

Implicit in these data, as edited, is the notion that the test period for efficiency related traits need be no longer than 8 wk. Test periods of greater duration obligate facilities with the opportunity cost derived from not testing additional boars. Evaluation of trade-offs associated with shorter test periods, in the context of genetic evaluation, is a potentially fruitful topic for further study. It should be noted that for evaluating phenotypic differences among animals, the critical phenotype in determining the length of the test is ADG rather than FI (Arthur et al. 2008). This observation is supported by results from substantially larger data sets examining effects on genetic prediction in cattle (Archer et al. 1997; Wang et al. 2006).

Descriptive statistics for production traits (ADG, WT, D100, LMD, and FAT) and FI are presented in Table 1. In general, the heritability estimates for FI, ADG, WT, and FAT were similar to those observed by Hoque and Suzuki (2008) for Duroc boars tested over an interval from approximately 30 to 90 kg. However, the heritability estimates for FI and ADG observed in this study were significantly greater than corresponding estimates for Duroc boars tested over 3-wk periods (Chen et al. 2010) and lower than Duroc boars tested for 45 d at an average start age of 85 d (Jiao et al. 2014). Heritability estimates for BF and LMD observed here were significantly less than those observed for BF and longissimus muscle area by Hoque et al. (2007) and Jiao et al. (2014), also for Duroc pigs. Heritability estimates for D100, FD and LMD were similar to unpublished estimates (Mwansa and Kemp, personal communication) of 0.22, 0.38 and 0.27, respectively, for a similar population but including all Duroc boars and gilts over a longer time period. Estimates of genetic and residual covariances among traits used in the prototype BLUP evaluation of FI are shown in Table 2. Estimates of the corresponding genetic and environmental correlations are shown in

**Table 1.** Numbers of records, means, estimated genetic and residual standard deviations, and heritability estimates ( $\pm$  SE) for average daily feed intake, average daily gain (ADG), mid-test weight, age at attaining 100 kg live weight<sup>z</sup>, and subcutaneous fat depth and longissimus muscle depth

Trait	N	Mean	Genetic SD	Residual SD	$h^2$
Feed intake (kg d <sup>-1</sup> )	3291	2.09	0.1442	0.2062	0.33 $\pm$ 0.05
ADG (kg d <sup>-1</sup> )	4651	0.94	0.0505	0.0827	0.27 $\pm$ 0.04
Mid-test weight (kg)	4651	72.0	3.9991	5.6486	0.33 $\pm$ 0.05
Age at 100 kg (d)	4542	151.1	6.1234	8.9516	0.31 $\pm$ 0.04
Fat depth (mm)	4542	11.3	1.4877	1.5926	0.47 $\pm$ 0.05
Longissimus depth (mm)	4542	59.8	2.5388	4.6808	0.23 $\pm$ 0.04

<sup>z</sup>Permanent environmental variance due to litters explained 2.8  $\pm$  1.2% of phenotypic variance.

**Table 2. Genetic (above diagonal) and environmental (below diagonal) covariances among average daily feed intake, age to attain 100 kg live weight, and fat depth measured at the end of the evaluation period**

Trait	FI	D100	FAT
Feed intake (FI) (kg d <sup>-1</sup> )		-0.7044	0.1258
Age at 100 kg (D100) (d)	-1.2050		-4.3583
Fat depth (FAT) (mm)	0.1446	-4.3583	

Table 3. Estimates of genetic and residual covariances from the BLUP analysis to derive measures of efficiency are shown in Table 4. Estimates of the corresponding genetic and residual correlations are shown in Table 5. The genetic correlations indicate stronger genetic antagonism between FI and ADG than was observed by Hoque and Suzuki (2008;  $r_g = 0.52$ ) and Jiao et al. (2014;  $r_g = 0.32$ ), suggesting that in this population the search for genetically more efficient pigs will be challenging. In the present study, LMD appeared genetically independent of both FI and FAT, with only modest correlations to ADG and WT. Jiao et al. (2014) reported a similar genetic correlation for LMD and FI; however, they reported a significantly higher correlation between LMD and FD (0.32) and a correlation of  $-0.21$  between LMD and ADG. The estimated genetic correlations of FI and ADG with FAT being equal to or greater than 0.5 are supported by previous observations (Hoque and Suzuki 2008). However, Jiao et al. (2014) reported lower correlation estimates of 0.36 and 0.22 for FAT with FI and ADG, respectively. Taken together, these results indicate opportunity to change body composition, particularly LMD, without increasing cost of production. Further, it appears there is opportunity to increase LMD while either not changing or even decreasing FAT. Von Felde et al. (1996) concluded that selection to improve efficiency of lean growth may be most efficient using an index of component traits. Here, such an index might include the EBV for FI, ADG, LMD and FAT.

Environmental conditions which support greater FI are also favorable for growth of both lean and fat. The estimated environmental correlations among FI, ADG, and FAT were of generally similar magnitude to the corresponding estimates of genetic correlation. However, the estimated environmental correlations of LMD with FI, ADG, MWT, and FAT were all greater than their genetic counterparts.

As derived from variances of the predictive linear functions, heritability estimates for RFI and RG were

**Table 3. Genetic (above diagonal) and environmental (below diagonal) correlations ( $\pm$  SE) among average daily feed intake, age to attain 100 kg live weight, and fat depth measured at the end of the evaluation period**

Trait	FI	D100	FAT
Feed intake (FI) (kg d <sup>-1</sup> )		$-0.80 \pm 0.05$	$0.57 \pm 0.08$
Age at 100 kg (D100) (d)	$-0.65 \pm 0.03$		$-0.47 \pm 0.09$
Fat depth (FAT) (mm)	$0.46 \pm 0.04$	$-0.49 \pm 0.04$	

**Table 4. Genetic (above diagonal) and environmental (below diagonal) covariances among average daily feed intake, average daily gain (ADG), mid-test weight, and fat depth and longissimus muscle depth measured at the end of the evaluation period**

Trait	FI	ADG	WT	FAT	LMD
Feed intake (FI) (kg d <sup>-1</sup> )		0.005750	0.4486	0.1258	0.05525
ADG (kg d <sup>-1</sup> )	0.01154		0.1650	0.03952	0.03577
Mid-test weight (WT) (kg)	0.8186	0.3720		2.321	4.191
Fat depth (FAT) (mm)	0.1446	0.05988	3.916		0.08492
Longissimus depth (LMD) (mm)	0.3773	0.1674	11.60	3.197	

0.22 and 0.21, respectively. These calculated heritabilities for RFI and RG were less than for FI and ADG, respectively. Similarly derived estimates of the part-whole genetic correlations of RFI with FI and RG with ADG were 0.53 and 0.61, respectively. As expected, the estimated genetic correlations of RFI with ADG, WT, and FAT were all 0.00. Likewise, the estimated genetic correlations of RG with FI and FAT were both 0.00. The genetic correlations of RFI and RG with LMD were  $-0.22$  and  $0.27$ , respectively. The correlation between RFI and LMD observed here was substantially weaker than the strong antagonistic correlation between RFI and longissimus muscle area found by Hoque et al. (2007).

For individual pigs and sires that were evaluated based on pedigree, those having data only for indicator traits, and those having recorded FI,  $R_{IH}$  for FI, RFI, and RG are summarized in Table 6. As a result of the lower heritability for efficiency measures compared with FI, accuracies were consistently less for the EBV of RFI and RG relative to the accuracy of the FI EBV. These data indicate less increase in accuracy due to having recorded feed intake than was observed by MacNeil et al. (2011) for Angus cattle. This difference may be attributable to the difference in relationship structure stemming in part from the greater full- and half-sib family sizes for pigs as compared with cattle. However, only through recording and analysis of feed intake does the opportunity present itself to identify those unique individuals whose EBV profiles break the genetic antagonism whereby greater growth requires greater feed intake.

## CONCLUSIONS

Heritability estimates for FI, D100, ADG, WT, FAT, and LMD were all of moderate magnitude indicating the opportunity to change these traits through genetic selection. The moderate to large genetic correlations of D100, ADG, WT, and FAT with FI indicate their value as indicator traits and in the calculation of efficiency measures. However, D100 is highly collinear with ADG and WT. Thus, these three indicators of growth should not be fit simultaneously in a single evaluation. Further, it should be noted that only through recording and analysis of feed intake does the opportunity present itself to identify those unique individuals whose EBV profiles

**Table 5.** Genetic (above diagonal) and environmental (below diagonal) correlations ( $\pm$  SE) among average daily feed intake, average daily gain, mid-test weight, and fat depth and longissimus muscle depth measured at the end of the evaluation period

Trait	FI	ADG	WT	FAT	LMD
Feed intake (FI) (kg d <sup>-1</sup> )		0.79 $\pm$ 0.05	0.78 $\pm$ 0.05	0.57 $\pm$ 0.08	0.15 $\pm$ 0.14
ADG (kg d <sup>-1</sup> )	0.68 $\pm$ 0.02		0.82 $\pm$ 0.04	0.53 $\pm$ 0.07	0.28 $\pm$ 0.11
Mid-test weight (WT) (kg)	0.70 $\pm$ 0.02	0.80 $\pm$ 0.01		0.39 $\pm$ 0.08	0.33 $\pm$ 0.05
Fat depth (FAT) (mm)	0.44 $\pm$ 0.04	0.45 $\pm$ 0.03	0.44 $\pm$ 0.04		0.02 $\pm$ 0.10
Longissimus depth (LMD) (mm)	0.39 $\pm$ 0.04	0.43 $\pm$ 0.03	0.44 $\pm$ 0.03	0.43 $\pm$ 0.03	

**Table 6.** Accuracy of genetic evaluations for feed intake (ACC<sub>FI</sub>), residual feed intake (ACC<sub>RFI</sub>) and residual gain (ACC<sub>RG</sub>) as functions of the available phenotypic data

Available data	N	ACC <sub>FI</sub>	ACC <sub>RFI</sub>	ACC <sub>RG</sub>
Pigs with only pedigree data	1364	0.61	0.42	0.47
Sires with only pedigree data	219	0.60	0.41	0.46
Pigs with pedigree and indicator trait data	1360	0.61	0.41	0.48
Sires with pedigree and indicator trait data	20	0.82	0.55	0.63
Pigs with complete records <sup>z</sup>	3291	0.67	0.45	0.50
Sires with complete records <sup>z</sup>	50	0.82	0.55	0.62

<sup>z</sup>Complete records are those with pedigree, indicator trait data, and feed intake recorded.

break the general genetic relationship of superior performance (output) requiring greater feed intake (input). Given, the magnitude of the genetic correlations of the growth traits with feed intake, breaking the genetic antagonism between growth and feed intake will be challenging in this population. An appropriate selection index of component traits likely provides greater opportunity to break this genetic antagonism than selection based on either efficiency measure.

#### ACKNOWLEDGEMENTS

The authors express their appreciation to the staff at the Daly Research and Development Facility, Mrs. Susan Linto for technical assistance, Mr. Mark Lowerison for database development and developments of edit procedures, and Dr. P. Mwansa for comments on the manuscript. We also acknowledge CanAm Genetics and Genesis Inc. for the financial support for this study.

**Archer, J. A., Arthur, P. F., Herd, R. M., Parnell, P. F. and Pitchford, W. S. 1997.** Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British breed cattle. *J. Anim. Sci.* **75**: 2024–2032.

**Arthur, P. F., Barchia, I. M. and Giles, L. R. 2008.** Optimum duration of performance tests for evaluating growing pigs for growth and feed efficiency traits. *J. Anim. Sci.* **86**: 1096–1105.

**Boldman, K. G., Kriese, L. A., VanVleck, L. D. and Kachman, S. D. 1993.** A manual for use of MTDFREML. USDA Agricultural Research Service, Clay Center, NE.

**Casey, D. S., Stern, H. S. and Dekkers, J. C. M. 2005.** Identification of errors and factors associated with errors in data from electronic swine feeders. *J. Anim. Sci.* **83**: 969–982.

**Chen, C. Y., Misztal, I., Tsuruta, S., Zumbach, B., Herring, W. O., Holl, J. and Culbertson, M. 2010.** Estimation of genetic parameters of feed intake and daily gain in Durocs using data from electronic swine feeders. *J. Anim. Breed. Genet.* **127**: 230–234.

**Conner, M. L. 1993.** Recommended code of practice for the care and handling of farm animals: Pigs. Publ. 1898/E. Agriculture and Agri-Food Canada, Ottawa, ON.

**Dodenhoff, J., Van Vleck, L. D., Kachman, S. D. and Koch, R. M. 1998.** Parameter estimates for direct, maternal and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* **76**: 2521–2527.

**Henderson, C. R. and Quaas, R. L. 1976.** Multiple trait evaluation using relatives' records. *J. Anim. Sci.* **43**: 1188–1197.

**Hoque, M. A. and Suzuki, K. 2008.** Genetic parameters for production traits and measures of residual feed intake in Duroc and Landrace pigs. *Anim. Sci. J.* **79**: 543–549.

**Hoque, M. A., Suzuki, K., Kadowaki, H., Shibata, T. and Oikawa, T. 2007.** Genetic parameters for feed efficiency traits and their relationships with growth and carcass traits in Duroc pigs. *J. Anim. Breed. Genet.* **124**: 108–116.

**Jiao, S., Maltecca, C., Gray, K. A. and Cassady, J. P. 2014.** Feed intake, average daily gain, feed efficiency, and real-time ultrasound traits in Duroc pigs: I. Genetic parameters estimation and accuracy of genomic prediction. *J. Anim. Sci.* **92**: 2377–2386.

**Johnson, D. L. and Thompson, R. 1995.** Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. *J. Dairy Sci.* **78**: 449–456.

**Kennedy, B. W., van der Werf, J. H. J. and Meuwissen, T. H. E. 1993.** Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* **71**: 3239–3250.

**Koch, R. M., Swiger, L. A., Chambers, D. and Gregory, K. E. 1963.** Efficiency of feed use in beef cattle. *J. Anim. Sci.* **22**: 486–494.

**MacNeil, M. D., Lopez-Villalobos, N. and Northcutt, S. L. 2011.** A prototype national cattle evaluation for feed intake and efficiency of Angus cattle. *J. Anim. Sci.* **89**: 3917–3923.

**Von Felde, A., Roehe, R., Looft, H. and Kalm, E. 1996.** Genetic association between feed intake and feed intake behaviour at different stages of growth of group-housed boars. *Livestk. Prod. Sci.* **47**: 11–22.

**Wang, Z., Nkrumah, J. D., Li, C., Basarab, J. A., Goonewardene, L. A., Okine, E. K., Crews, D. H. Jr. and Moore, S. S. 2006.** Test duration for growth, feed intake, and feed efficiency in beef cattle using the GrowSafe system. *J. Anim. Sci.* **84**: 2289–2298.