

ANIMAL GENETICS AND GENOMICS

Genetic associations between stayability and longevity in commercial crossbred sows, and stayability in multiplier sows

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Abstract

Longevity in commercial sows is often selected for through stayability traits measured in purebred animals. However, this may not be justifiable because longevity and stayability may be subject to both genotype by environment interaction ($G \times E$) and genotype by genotype interaction ($G \times G$). This study tested the hypothesis that stayability to service after first parity is more strongly genetically correlated with longevity in commercial herds when stayability is measured in commercial herds rather than multiplier herds. The analysis was based on farrowing- and service-records from 470,824 sows (189,263 multiplier; 281,561 commercial) and 300 herds (156 multiplier; 144 commercial sows). Multiplier sows were either purebred Landrace or Yorkshire and commercial sows were mainly rotationally crossbreds between the two breeds. Commercial longevity was defined as age in days when culled (**LongC**), and stayability to service after first parity was defined for both commercial sows (**StayC**) and multiplier sows (**StayM**). The genetic correlations between LongC, StayC, and StayM were estimated by restricted maximum likelihood using linear mixed models. Genetic parameters were estimated separately for Landrace and Yorkshire. In Landrace, the genetic correlations between LongC and StayC, LongC and StayM, and StayC and StayM were 0.86 ± 0.02 , 0.24 ± 0.05 , and 0.34 ± 0.06 , respectively. In Yorkshire, the genetic correlations between LongC and StayC, LongC and StayM, and StayC and StayM were 0.81 ± 0.03 , 0.17 ± 0.05 , and 0.18 ± 0.07 , respectively. Conclusively, longevity in commercial herds is more strongly correlated with stayability when stayability is measured in commercial herds rather than multiplier herds.

Key words: association, crossbreeding, genetic, heterosis, longevity, stayability

Introduction

Longevity in commercial sows is favorably associated with both economic profit and animal welfare. Economic studies show that commercial sows should succeed 6 to 10 parities prior to their replacement (Dijkhuizen et al., 1986; Dhuyvetter, 2000; Gruhot et al., 2017; SEGES, 2019). Nevertheless, commercial

sows on average only succeed 3 to 5 parities as they are culled prematurely due to, for example, reproductive disorders (26.9%), udder problems (18.1%), low productivity (9.5%), and lameness (8.6%) (Rodriguez-Zas et al., 2003; PigChamp, 2004; Engblom et al., 2007; Hong et al., 2019). Consequently, the economic potential of commercial sows is not fully realized. Furthermore, several of the reasons for which sows are culled are marked as indicators

Abbreviations

EBV	estimated breeding value
HYM	interaction level between herd, year, and month
LongC	age in days when culled for sows in commercial breed-to-wean herds (d)
StayC	stayability to service after first parity for sows in commercial breed-to-wean herds
StayM	stayability to service after first parity for sows in multiplier herds

of poor animal welfare (Welfare Quality, 2009), and sows that are predisposed for conditions related to poor animal welfare most likely have shorter lives. Therefore, the improvement of longevity in commercial sows will most likely improve both the economic profit and animal welfare on commercial farms.

It is challenging to improve longevity in commercial sows through direct selection (Serenius and Stalder, 2006; Engblom et al., 2009; Tart et al., 2013). First, it takes a long time before phenotypes on longevity are available, with the implications of both right censoring and a weak relationship between phenotyped sows and selection candidates. Second, longevity is most likely subject to genotype by environment interaction ($G \times E$) as it is heavily dependent on culling strategies and environmental stressors, both of which are expected to vary between commercial herds. Third and last, it is uncommon for breeding companies to have access to phenotypes for longevity in commercial herds. To avert some of these challenges, some breeding companies instead indirectly select for increased longevity in commercial sows through stayability traits that are measured early-in-life of nucleus- or multiplier-sows (Ask, 2015; Karlsson, 2018).

The advantages of indirect selection for longevity in commercial herds through early-in-life stayability in nucleus- or multiplier-sows are: 1) possibly stronger genetic relationships between phenotyped sows and selection candidates, 2) no/limited right-censoring, 3) better data quality, 4) better data availability, and 5) a strong theoretical framework for genetic analysis of purebred animals. However, stayability from these herd types may not be adequately genetically correlated with longevity in commercial sows (Abell et al., 2016), especially since what constitutes longevity is affected by the culling strategy. For example, the culling strategies in nucleus- or multiplier-herds ensure the production of genetically superior animals, while the culling strategies in commercial herds ensure that piglets are produced at the lowest cost possible. Consequently, the biological background for indicator traits from nucleus- or multiplier-herds most likely differs from the biological background for longevity in commercial sows ($G \times E$). Furthermore, commercial sows are often crossbred which may affect the genetic background for longevity genotype by genotype interaction ($G \times G$) (Wei et al., 1991). Since longevity may be subject to both $G \times E$ and $G \times G$, it is likely that stayability is more strongly associated with longevity in commercial sows if stayability is measured in commercial herds instead of nucleus- or multiplier-herds.

We hypothesized that stayability to service after first parity is more strongly genetically correlated with longevity in commercial sows when stayability is measured in commercial sows rather than multiplier sows.

Materials and Methods

Animal Care and Use Committee approval was not obtained for this study as data were obtained from an existing database.

To test the hypothesis, genetic correlations between age when culled in commercial herds (LongC; continuous trait), stayability to service after first parity in commercial herds (StayC; binary trait), and stayability to service after first parity in multiplier herds (StayM; binary trait) were simultaneously estimated using two tri-variate linear mixed models—one model for each of the breeds (Landrace and Yorkshire). The analysis was based on the data from DanBred multiplier herds and Danish commercial breed-to-wean herds.

Phenotype data

The data from multiplier herds were obtained from purebred Landrace or Yorkshire sows through standard DanBred breeding procedures. The data from the commercial breed-to-wean herds were obtained through the Nucleus Management software (DanBred, 2019). Nucleus Management is a management tool that assists commercial farmers with on-farm selection of females by providing farmers with the genetic merits of their commercial sows. Commercial sows are either purebred, F1 crossbred, or rotationally crossbred.

Farrowing records from both multiplier sows and commercial sows born between January 1, 2010, and December 31, 2014, were provided by Breeding & Genetics, SEGES, Denmark. In total, 300 herds (156 multiplier; 144 commercial) and 470,824 sows (189,263 multiplier; 281,561 commercial) passed the quality control (see section below) (Table 1).

Quality control of phenotype data

The quality control of phenotype data was performed at two levels: first at herd-level and then at sow-level. The data from commercial herds were quality controlled at both levels. The data from multiplier herds were only quality controlled at the animal level since these herds have followed strict guidelines for providing data.

The purpose of quality control at herd-level was to find commercial herds that provide valid data for the analysis. The ability of commercial herds to consistently provide valid data was determined by (Table 2): 1) Selecting age at first farrowing, farrowing interval, parity number, Identity of father of sow, and farrowing with Duroc sire as critical variables; 2) Selecting accepted values or intervals for each critical variable; 3) Calculating the fraction of each critical variable that is accepted within each herd; 4) Selecting the minimum for the fraction of accepted observations for each critical variable; and 5) Filtering away herds where the fraction of accepted observations was less than required for one or more critical variable(s). The remaining herds were used for further analysis if they recorded more than 150 farrowings each year.

The purpose of quality control at sow-level was to remove sows with untrusted measurements within trusted herds.

Table 1. Number of herds, fathers of sows, and sows included in the analysis

	Commercial	Multiplier	Shared
Herds	144	156	0
Fathers of sows (all)	5,739	3,254	3,113
Fathers of sows (Landrace)	2,580	1,562	1,502
Fathers of sows (Yorkshire)	3,159	1,692	1,611
Sows and gilts (all)	281,561	189,263	0
Sows and gilts (Landrace)	2,905	107,076	0
Sows and gilts (Yorkshire)	1,016	82,187	0
Sows and gilts (Crossbred)	277,640	0	0

Table 2. Critical values for herd-level quality control in commercial herds

Critical value	Accepted value or interval	Min. fraction of accepted observations, %
Age at first farrowing, d	[300; 460]	90
Farrowing interval, d	[120; 232]	95
Parity number	Is equal to a predicted parity number (see Supplementary Appendix)	90
ID of father of sow	Is known	95
Farrowing with Duroc sire	Is true	80

Sows were kept for further analysis if: the sow only produced litters in the herd it was born in, and this herd was marked as providing valid observations; at least 90 % of the genetic make-up was Landrace and/or Yorkshire (this requires at least four generations with pedigree-information); and age at first farrowing was less than 460 d.

Constructing covariates

Commercial breed-to-wean sows can be crossbred at any ratio between Landrace and Yorkshire. The breed difference between sows may give rise to both breed effects and heterosis effects that should be accounted for by the statistical model (Falconer and Mackay, 1996). To quantify the two genetic effects, first, the fractions of Yorkshire and Landrace in the commercial sows were calculated based on pedigree information, and second, the expected levels of heterosis in sows were calculated as: $\text{heterosis} = 1 - \text{abs}(2 \times Y - 1)$, where Y is the fraction of Yorkshire in the sow, and is the absolute of the value. The fraction of Yorkshire was chosen as the only measure for breed fraction as the fractions of Landrace and Yorkshire were almost perfectly interdependent. Neither breed fraction nor heterosis was calculated for multiplier sows as these are all purebred.

Culling decisions, and thereby longevity, are affected by the reproductive performance of the sows (Engblom et al., 2007). However, in this study, we were interested in longevity independent from the reproductive performance. Therefore, we needed a measure of the reproductive performance of sows to account for the effect of litter size on longevity. For StayC and StayM, only the litter size in first parity was known when the phenotype was realized. Therefore, the reproductive performance of a sow was defined as the deviation in total number born in first parity from the mean total number born of first parity sows within the relevant combination of herd and year. For LongC, possibly multiple reproductive performances were known when the phenotype was realized. Therefore, the reproductive performance of sows was defined as the predicted random sow effect on litter size across parities g estimated using a linear mixed model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wg} + \mathbf{e},$$

where \mathbf{y} is a vector of observations on total number born across all parities; \mathbf{b} is a parameter vector of the fixed class effects of herd, birth year, birth month, and parity number; \mathbf{g} is a vector of random sow effects; \mathbf{e} is a vector of residual effects; and \mathbf{X} and \mathbf{W} are design matrices. The random sow effect and

residual were assumed to be identically and independently normal distributed with each their respective variances. The reproductive performances of multiplier sows and commercial sows were predicted separately.

Breed-specific pedigrees

The breed-specific pedigrees were constructed by first tracing an overall pedigree from the phenotyped sows. This overall pedigree contained both Landrace pigs, Yorkshire pigs, and crossbred pigs due to the crossbreeding procedure in commercial herds. Second, from this overall pedigree, two breed-specific pedigrees were constructed: one for pigs with Landrace heritage and one for pigs with Yorkshire heritage; i.e., each breed-specific pedigree contains both purebred- and crossbred-animals. To construct the Landrace-specific pedigree, purebred Yorkshire sires and dams were marked as unknown and removed from the pedigree together with their purebred ancestors. The same procedure was used for constructing the Yorkshire-specific pedigree. Note that crossbred animals are treated as purebred animals in the pedigree. Summary statistics for both phenotypes and covariates are shown in Table 3.

Statistical models

LongC, StayC, and StayM were simultaneously analyzed using a three-trait linear mixed model, separately for each breed:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_3 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{W}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{W}_3 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{u}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix},$$

where subscripts 1, 2, and 3 indicate LongC, StayC, and StayM, respectively; \mathbf{y}_1 , \mathbf{y}_2 , and \mathbf{y}_3 are vectors with phenotypes for sows; \mathbf{b}_1 , \mathbf{b}_2 , and \mathbf{b}_3 are parameter vectors for the fixed effects of herd, year at birth, month at birth, fraction of Yorkshire genes in the sow (only included for subscripts 1 and 2), fraction of heterosis in the sow (only included for subscripts 1 and 2), age at first farrowing; age at first farrowing squared, and reproductive performance; \mathbf{a}_1 , \mathbf{a}_2 , and \mathbf{a}_3 are vectors of additive genetic effects; \mathbf{u}_1 , \mathbf{u}_2 , and \mathbf{u}_3 are vectors with the interaction effects of herd, year, and month at birth (HYM); \mathbf{e}_1 , \mathbf{e}_2 , and \mathbf{e}_3 are vectors of residual effects; and \mathbf{X} , \mathbf{Z} , and \mathbf{W} are design matrices.

The two statistical models contain nine random effects; three genetic-, three HYM-, and three residual effects. The three random genetic effects were assumed to be distributed as:

$$\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} \sim \text{MVN} \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_{A1}^2 & \cdot & \cdot \\ \sigma_{A2,A1} & \sigma_{A2}^2 & \cdot \\ \sigma_{A3,A1} & \sigma_{A3,A2} & \sigma_{A3}^2 \end{bmatrix} \otimes \mathbf{A} \right),$$

where σ_{A1}^2 is the additive genetic variance for LongC; σ_{A2}^2 is the additive genetic variance for StayC; σ_{A3}^2 is the additive genetic variance for StayM; and $\sigma_{A2,A1}$, $\sigma_{A3,A1}$, and $\sigma_{A3,A2}$ are covariances; \mathbf{A} is either the Landrace-specific or the Yorkshire-specific pedigree, and \otimes is the Kronecker product. The three random HYM effects were assumed to be distributed as:

$$\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{u}_3 \end{bmatrix} \sim \text{MVN} \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_{U1}^2 & \cdot & \cdot \\ \sigma_{U2,U1} & \sigma_{U2}^2 & \cdot \\ \mathbf{0} & \mathbf{0} & \sigma_{U3}^2 \end{bmatrix} \otimes \mathbf{I} \right),$$

where $\sigma_{U_1}^2$ is the HYM variance for LongC; $\sigma_{U_2}^2$ is the HYM variance for StayC; $\sigma_{U_3}^2$ is the HYM variance for StayM; σ_{U_2, U_1} is a covariance; \otimes is the Kronecker product; and I represents two different identity matrices with dimensions equal to the number of levels of either u_1 (identical to the number of levels of u_2) or u_3 .

The three random residual effects were assumed to be distributed as:

$$\begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix} \sim \text{MVN} \left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_{E_1}^2 & & \\ \sigma_{E_2, E_1} & \sigma_{E_2}^2 & \\ 0 & 0 & \sigma_{E_3}^2 I \end{bmatrix} \otimes I \right),$$

where $\sigma_{E_1}^2$ is the residual variance for LongC; $\sigma_{E_2}^2$ is the residual variance for StayC; $\sigma_{E_3}^2$ is the residual variance for StayM; σ_{E_2, E_1} is a covariance; \otimes is the Kronecker product; and I represents two different identity matrices with dimensions equal to the number of levels of either e_1 (identical to the number of levels of e_2) or e_3 .

(Co)variance components were estimated using the average-information restricted maximum likelihood algorithm in the DMU software (Madsen and Jensen, 2013). The standard errors of (co)variance components were approximated using their asymptotic normal distribution. The standard errors of heritability statistics, correlations, and differences between correlations were approximated with the Delta Method (Dorfman, 1938; Oehlert, 1992); i.e., using the asymptotic (co)variance matrix of parameters estimates. The standard errors of differences between variance components from Landrace and Yorkshire were calculated as: $SE_{\text{difference}} = \sqrt{SE_{\text{Landrace}}^2 + SE_{\text{Yorkshire}}^2}$, where SE is a standard error, and subscripts denote whether the standard error is for the variance component from Landrace, Yorkshire, or the difference between the two. Note that this approach assumes that estimates of variance components are independently distributed across

breeds. Statistical significances (P -value < 0.05) were calculated by assuming that standard errors are normally distributed.

Note on the discussion of stayability traits

No other study analyzed the stayability to service after first parity. Instead, other studies more frequently analyzed stayability to second parity (Engblom et al., 2009; Le et al., 2015, 2016; Abell et al., 2016). However, the vast majority of sows are removed at the end of the lactation period (Engblom et al., 2007); i.e., prior to/during the farmer decision for the service of sows. Therefore, we interchangeably use genetic parameters for stayability to service after first parity and stayability to second parity in the discussion.

Results

Genetic correlations, phenotypic correlations, and heritabilities are presented in Table 4; differences between genetic correlations are presented in Table 5; variance components are presented in Table 6; estimated regression coefficients are presented in Table 7.

Genetic correlations

In Landrace, the genetic correlations between LongC and StayC, LongC and StayM, and StayC and StayM were 0.86 ± 0.02 , 0.24 ± 0.05 , and 0.34 ± 0.06 , respectively. In Yorkshire, the genetic correlations between LongC and StayC, LongC and StayM, and StayC and StayM were 0.81 ± 0.03 , 0.17 ± 0.05 , and 0.18 ± 0.7 , respectively. Genetic correlations were numerically larger for Landrace than for Yorkshire.

LongC was more strongly genetically correlated with StayC than StayM (Landrace: $+0.63 \pm 0.06$, P -value: 0.00; Yorkshire: $+0.64 \pm 0.06$, P -value: 0.00). StayM was more strongly genetically correlated with StayC than LongC in Landrace

Table 3. Descriptive statistics for covariates and response variables

Variable	Commercial				Multiplier ¹			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Stayability to service after first parity	0.85	0.36	0.00	1.00	0.80 0.81	0.40 0.40	0.00 0.00	1.00 1.00
Age when culled, d	858.4	317.1	156.0	3027.0				
Fraction of Yorkshire	0.49	0.18	0.00	1.00				
Fraction of heterosis	0.68	0.16	0.00	1.00				
Age at first farrowing, d	369.8	28.0	128.0	459.0	372.0 378.7	31.5 30.7	251.0 252.0	459.0 459.0
Reproductive performance (first), #piglets	0.0	3.4	-16.0	19.5	0.0 0.0	3.8 3.8	-15.9 -15.1	19.7 18.7
Reproductive performance (all), #piglets	0.0	2.2	-11.7	10.4				

¹Each cell has two numbers. The top number is based on Landrace data while the bottom number is based on Yorkshire data.

Table 4. Heritabilities (diagonal/bold), genetic correlations (below diagonal), and phenotypic correlations (above diagonal) for LongC, StayC, and StayM

	Landrace			Yorkshire		
	LongC	StayC	StayM	LongC	StayC	StayM
LongC	0.06 ± 0.00	0.62 ± 0.00	0.03 ± 0.01	0.05 ± 0.00	0.62 ± 0.00	0.02 ± 0.01
StayC	0.86 ± 0.02	0.02 ± 0.00	0.02 ± 0.00	0.81 ± 0.03	0.01 ± 0.00	0.01 ± 0.00
StayM	0.24 ± 0.05	0.34 ± 0.06	0.21 ± 0.01	0.17 ± 0.05	0.18 ± 0.07	0.29 ± 0.01

(0.11 ± 0.04 , P -value: 0.02) but equally so in Yorkshire (0.11 ± 0.04 , P -value: 0.92).

StayM was 0.11 ± 0.04 more strongly genetically correlated with StayC than with LongC in Landrace, but equally so in Yorkshire.

Variance components

The additive genetic variances for LongC and StayC were greater for Landrace than for Yorkshire (5,983 vs. 4,595, P -value: 0.01; and 2.7 vs. 1.9, P -value: 0.05) while the additive genetic variance for StayM was greater for Yorkshire than for Landrace (40.1 vs. 32.2, P -value: 0.01). For both Landrace and Yorkshire, the additive genetic variance for StayM was 29.5×10^{-3} – 38.2×10^{-3} greater than the additive genetic variance for StayC (P -values: 0.00) despite having similar phenotypic variances (P -values: >0.95). The phenotypic variance for StayM differed between breeds (P -value: 0.00).

Regression coefficients

All estimated regression coefficients for LongC and StayC, but not StayM, were similar between the two analyses of breeds. The regression coefficients for the fraction of Yorkshire in the sows (35.2 ± 11.5 – 38.3 ± 11.5) and fraction of heterosis (144.5 ± 4.3 – 143.4 ± 4.3) were favorably associated with both LongC and StayC. Increased age at first farrowing increased LongC, StayC, and StayM for Landrace. On the contrary, increased age at first farrowing was associated with lower StayM for Yorkshire. Reproductive performance was favorably associated with both LongC, StayC, and StayM for both breeds.

Discussion

As hypothesized, StayC was more strongly genetically correlated with LongC than StayM ($+0.63 \pm 0.06$ – 0.64 ± 0.06). In fact, StayM was only low to moderately genetically correlated with LongC (0.17 ± 0.05 – 0.24 ± 0.05) while StayC was highly so (0.81 ± 0.03 – 0.86 ± 0.02). The latter was expected due to the phenotypic dependency of LongC on StayC; i.e., only sows that were serviced after first parity (above-average StayC) could achieve

above-average levels of LongC. The low to moderate positive genetic correlation between StayC and StayM indicates that the environments for sows differ sufficiently across types of herds to change the underlying genetic backgrounds of two otherwise similar longevity-related traits.

Genetic correlations across herd types

The genetic correlation between StayC and StayM was low to moderate (0.18 ± 0.07 – 0.34 ± 0.0). Abell et al. (2016) estimated similar genetic correlations (across purebreds and crossbreds, and herd types) and found that stayability to second parity was 0.38 ± 0.30 genetically correlated between purebred nucleus sows and crossbred commercial sows. However, their study was based on information from only five nucleus herds and two commercial herds; all of which were owned by the same company and followed the same management protocols (Abell et al., 2016). Furthermore, Abell et al. (2016) report that only a few sires were used in both nucleus herds and multiplier herds. Consequently, their standard error is large, and their genetic correlations may be large due to the universal guidelines for management across herd types. This study was based on information from all relevant DanBred multiplier herds ($N = 156$) and many commercial herds ($N = 144$). Thereby, it is likely that the results on genetic correlations from this study better represent the general situation, and that genetic correlations for early stayability traits, in general, are less genetically associated between purebred pigs and crossbred pigs than previously reported.

Genetic correlations across traits

LongC and StayC were strongly genetically correlated. This complies with the results from previous studies where the genetic correlation between stayability to second parity and age when culled (or traits strongly genetically associated to this) was between 0.62 and 0.95 (Engblom et al., 2009; Aasmundstad et al., 2014; Le et al., 2015, 2016). This pattern has been seen regardless of whether sows are crossbred (Engblom et al., 2009) or purebred (Aasmundstad et al., 2014; Le et al., 2015, 2016). So, this implies that the choice of longevity-related phenotype is less crucial than the environment it is recorded in.

Heritability across herd type

The scientific literature generally reports larger heritabilities than those found by this study. There can be many reasons for the different estimates in different studies, e.g., actual differences between population parameters, sampling variance, and different methodologies. For example, Abell et al. (2016) and Sobczykńska et al. (2012) included the triple interaction of HYM of last farrowing as a fixed effect rather than as a random effect. This methodology effectively removes herd-specific seasonal variation from the denominator of the equation for the

Table 5. Differences between genetic correlations

Genetic correlations ¹	Landrace		Yorkshire	
	Difference ± SE	P -value	Difference ± SE	P -value
$\rho_{A1,A2}$ & $\rho_{A1,A3}$	0.63 ± 0.06	0.00	0.64 ± 0.06	0.00
$\rho_{A1,A2}$ & $\rho_{A2,A3}$	0.52 ± 0.07	0.00	0.63 ± 0.08	0.00
$\rho_{A1,A3}$ & $\rho_{A2,A3}$	0.11 ± 0.04	0.02	0.01 ± 0.05	0.92

¹A1, age in days when culled in a commercial herd. A2, stayability to service after first parity in a commercial herd. A3, stayability to service after first parity in a multiplier herd.

Table 6. Estimated variance components for LongC, StayC, and StayM

	Landrace			Yorkshire		
	LongC	StayC, 10^{-3}	StayM, 10^{-3}	LongC	StayC, 10^{-3}	StayM, 10^{-3}
σ_A^2	$5,983 \pm 42$	2.7 ± 0.3	32.2 ± 1.9	$4,595 \pm 347$	1.9 ± 0.3	40.1 ± 2.1
σ_U^2	$3,341 \pm 101$	3.2 ± 0.1	11.0 ± 0.4	$3,343 \pm 102$	3.2 ± 0.1	10.2 ± 0.5
σ_E^2	$85,468 \pm 469$	122.8 ± 0.4	107.9 ± 1.7	$86,849 \pm 412$	123.5 ± 0.4	88.9 ± 1.9
σ_P^2	$94,792 \pm 260$	128.6 ± 0.3	151.1 ± 0.8	$94,788 \pm 260$	128.6 ± 0.3	139.2 ± 0.8

¹ σ_P^2 , phenotypic variance.

Table 7. Estimated regression coefficients (\pm standard errors) for covariates related to Landrace (top in cells) and Yorkshire (bottom in cells) models

Variable	LongC	StayC, 10 ⁻²	StayM, 10 ⁻²
Fraction of Yorkshire	35.2 (\pm 11.5)	3.7 (\pm 1.3)	
	38.3 (\pm 11.5)	4.0 (\pm 1.3)	
Fraction of heterosis	144.5 (\pm 4.3)	11.1 (\pm 0.5)	
	143.4 (\pm 4.3)	11.0 (\pm 0.5)	
Age at first farrowing	2.37 (\pm 0.36)	0.15 (\pm 0.04)	0.03 (\pm 0.09)
	2.39 (\pm 0.36)	0.15 (\pm 0.04)	-0.30 (\pm 0.07)
Age at first farrowing squared	-0.0028 (0.0005)	-0.0003 (0.0001)	-0.0002 (0.0001)
	-0.0028 (0.0005)	-0.0003 (0.0001)	0.0002 (0.0001)
Reproductive performance	19.8 (\pm 0.2)	0.8 (\pm 0.0)	1.4 (\pm 0.0)
	19.8 (\pm 0.2)	0.8 (\pm 0.0)	1.4 (\pm 0.0)

heritability which may increase their heritability by design. In addition, previous studies with information from fewer herds tend to report larger estimated heritabilities for longevity-related traits than studies with information from many herds (Engblom et al., 2009; Sprangers et al., 2010; Sobczyńska et al., 2012; De Hollander et al., 2015; Le et al., 2015, 2016; Abell et al., 2016; Hong et al., 2019). This may be due to more similar culling strategies and management procedures among the few chosen herds which create a more consistent biological- and genetic-background for longevity-related traits across herds. Consequently, it is important to verify that the genetic analysis is based on a sample that is representative of the population of interest. Because of the implication of sample size on heritability estimation, only heritability estimates from studies with more than 14 herds are discussed in detail below.

The heritabilities from this study are to some extent in accordance with those from other studies with more than 14 herds. For purebred sows, these studies report that stayability to second parity is 0.08 – 0.22 (avg: 0.13) heritable (Le et al., 2015, 2016). In contrast, this study reported that stayability to service after first parity was 0.21 – 0.29 heritable for purebred animals. For crossbred sows, Engblom et al. (2009) reported that stayability to second parity was 0.03 to 0.04 (avg: 0.04) heritable while this study found that stayability to service after first parity was 0.01 – 0.02 heritable. Furthermore, Sobczyńska et al. (2012) reported that age when culled was 0.10 heritable for purebred sows while this study found that it was 0.05 – 0.06 heritable for crossbred sows. Thereby, both this and other studies agree that heritabilities for traits in crossbred sows are lower than those for traits in purebred sows. The lower heritabilities in crossbred sows may be because crossbred sows in both this and other studies primarily reside within commercial herds which are more diverse than nucleus herds and multiplier herds. The diversity of commercial herds may give rise to greater environmental variances and thereby lower heritabilities. This can also explain why the estimated heritabilities for age when culled are lower for this study than that for Sobczyńska et al. (2012). The greater heritabilities for purebred sows may also be explained by the existence of different culling strategies between types of herds. For example, nucleus- or multiplier-sows were more likely to be culled after first parity than commercial sows (0.85 vs. 0.80 – 0.81; P-values: 0.00). Since all sows in this analysis produced at least one litter, this difference mainly reflects the voluntary culling by the farmer. Thereby, the heritabilities for early stayability in nucleus- or multiplier-herd may be larger due to a greater proportion of voluntary culling and more consistent culling strategies, for example, culling of sows with low genetic merits.

Defining longevity through correction for fixed effects

In any study, the definition of the estimated breeding values (EBV) for longevity is defined by both the phenotype and the effects for which the phenotype is corrected. For example, in some studies, phenotypes are only corrected for herd and time effects (Engblom et al., 2009; Sevón-Aimonen and Uimari, 2013; Abell et al., 2016; Le et al., 2016) and the definition of the EBV is: EBV for longevity across herd and time. However, this definition of longevity may be too simple if the objective is to select for more resilient sows. For example, some sows are culled according to their reproductive performance (Engblom et al., 2007), which also indicated by the positive regression estimates for reproduction performance in this study. Thereby, not correcting the phenotype for reproductive performance allows EBVs for longevity to be influenced by this. However, ignoring reproductive performance in genetic evaluation for longevity is not desirable in most breeding programs as information on reproductive performance already is included in breeding indices. Therefore, we advise that longevity is corrected for the reproductive performance of sows when the objective is to increase longevity in breeding programs independently from reproductive performance.

Estimation of genetic parameters in crossbred animals

This study estimated genetic variances for Landrace and Yorkshire separately, even though the commercial sows were crossbreds between Landrace and Yorkshire. However, this approach is not theoretically correct. The implicit assumption in this study was that parents of the opposite breed than the breed of interest were randomly drawn from the base population of the breed of interest; i.e., their genetic effects are normally distributed with variance equal to that of the breed of interest. This is similar to the assumptions for a sire model. Wei et al. (1991) argued that it may be incorrect to assume that animals from other breeds are subject to similar genetic variances. In fact, this study shows that additive genetic variances may differ between breeds and that this assumption may be violated. In addition, marking other-breed parents as unknown may have caused the genetic variances to be more similar across breed than they are. Furthermore, crossbred animals beyond the F1 generation are subject to segregation effects that arise from differences in allele frequencies between contributing purebred populations (Lo et al., 1993). Such effects were not accounted for in this study because: 1) fathers of sows were purebred and most mothers of commercial sows were rotationally crossbred, which decreases the potential segregation variance by at least 50 % and 2) most

mothers of sows were the result of rotational crossbreeding which makes sows receive a somewhat equal contribution for segregation variance. Nevertheless, the theoretically correct approach is to simultaneously estimate genetic variances for all breeds while accounting for segregation variance(s) (Lo et al., 1993). Future studies may benefit from simultaneously estimating all genetic parameters for commercial longevity across breeds.

Alternatives to historical, uncensored longevity, and stayability

This study estimated genetic parameters for longevity in historical sows rather than recent and living sows. Thereby, no sows in this study had censored observations. However, analyzing historical sows is not advisable for practical implementation in a breeding program since phenotyped sows and selection candidates then are less likely to be closely related. Instead, it may be beneficial to use survival analysis models (Ducrocq and Casella, 1996; Maia et al., 2014), random regression models (Veerkamp et al., 2001), or threshold models to handle censored and/or binary longevity-related phenotypes from younger animals for practical implementation (See [Supplementary Material](#) for Model Validation Figures).

Quality control of data

The quality control at the herd-level filtered away two-thirds of the commercial herds in the initial dataset. This has most likely affected the estimated parameters, especially, if the herds which were filtered away represent a different type of herd than those herds which were not filtered away. Nevertheless, the comprehensive quality control was necessary for this study as it was crucial that all parities were reported for all sows.

Conclusion

Stayability to service after first parity was more strongly genetically correlated with longevity in commercial sows when stayability was measured in commercial sows (Landrace: 0.86 ± 0.02 ; Yorkshire: 0.81 ± 0.03) rather than multiplier sows (Landrace: 0.24 ± 0.05 ; Yorkshire: 0.17 ± 0.05).

Implications

The results from this study show that the genetic background for avoiding culling and achieving high longevity differs between types of herds. Consequently, pig breeding companies that aim to improve sow longevity should consider whether they are getting the genetic progress for the phenotype in commercial herds that they are expecting. Furthermore, the imperfect genetic correlation between longevity in commercial herds and the indicator trait for longevity in the breeding goal should be accounted for when calculating index weights, especially when using the Desired Gains approach.

Supplementary Data

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

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Conflict of interest statement

The authors declare that they have no conflict of interests.

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