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Genetic parameters for linear conformation, stayability, performance and reproduction traits in German local Swabian-Hall landrace sows

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Abstract

Improvements of longevity in sows are of overriding importance from an animal welfare as well as from an economic perspective, also in the local Swabian-Hall Landrace (SHL) breed. Consequently, the aim of the present study was a detailed assessment of linear conformation traits in the context of early predictions of sow stayability and to infer genetic (co)variance components between conformation traits with reproduction and performance traits. In this regard, we implemented a linear 9-point scoring system for conformation traits reflecting the body morphology and feet and leg characteristics in gilts. Linear conformation trait scoring included body length (BLEN), body height (BHEI), hind leg angularity (HLANG), hind leg pastern (HLPAS), hind cannon bone strength (HCBS), hind leg position (HLPOS), front leg position (FLPOS), claw length (CLEN) and muscling (MUSC) from 6042 SHL gilts before first insemination at the age of 180–200 days. For the same gilts, performance traits included average daily gain (ADG) and back fat thickness (BF) measured via ultrasound, reproduction traits included the number of piglets born alive (NBA) and the number of piglets weaned (NWEAN), and stayability was a binary trait reflecting sow survival after parity 2 (STAY_12), 3 (STAY_13) and 4 (STAY_14). For the estimation of variance components and heritabilities, single-trait linear animal models were defined for conformation, performance and reproduction traits, and single-trait generalized linear mixed models with a logit link function for binary stayability traits. Genetic covariances and correlations were inferred in series of bivariate runs for all combinations of conformation and remaining traits. The distribution of the assigned conformation scores reflected a Gaussian distribution, but a large fraction of records was assigned to the intermediate score classes 4, 5 and 6. Accordingly, the restricted utilization of the 9-point scale might explain the small genetic variances and small heritabilities for feet and leg traits in the range from 0.06 to 0.17. Heritabilities were larger for the linear traits reflecting body morphology, i.e., for BLEN (0.21) and BHEI (0.20). For conformation traits, the common litter environment explained up to 17% of the phenotypic trait variation. Genetic and especially

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phenotypic correlations between linear conformation traits with the reproduction traits NBA and NWEAN were close to zero. Heritabilities for STAY_12, STAY_13 and STAY_14 were 0.08, 0.07 and 0.05, respectively. Moderate genetic relationships were estimated between STAY_14 with some conformation traits. Especially high scores for BHEI and BLEN (i.e., long and large gilts) implied a decline in STAY_14 genetically ($r_g = -0.24$ and -0.53, respectively). Moderate genetic correlations were estimated between HLANG with STAY_14 (0.28), and between HCBS with STAY_12 (0.23). For most of the conformation traits with intermediate optimum, genetic correlations with STAY were close to zero, indicating improved longevity for gilts representing the population average with scores 4, 5 or 6, and suggesting the development of appropriate selection indices in this regard.

KEYWORDS

genetic parameters, linear conformation traits, local pig breed

1 | INTRODUCTION

The local the pig breed Swabian-Hall Landrace (SHL) as a new synthetic breed was established in southwestern Germany by crossing local Landrace boars with Chinese Meishan sows at the beginning of the 19th century, aiming on fertility improvements and local meat market requirements (Bühler, 1999). After the Second World War, there was an increasing demand for lean meat percentage, favouring efficient hybrid pig lines with lower intramuscular and back fat content. Such change in meat consumption preferences almost contributed to the extinction of the SHL breed. In 1990, private passionate SHL breeders implemented specific marketing strategies with focus on meat quality traits, which preserved the SHL and increased their population size step wisely (Petig, 2020). Genetic improvements also considered the production traits for female fertility (especially litter size) and piglet birth weights. Accordingly, genetic evaluations for female fertility in the SHL breed based on genetic parameters estimated in conventional pig breeds (Ferraz & Johnson, 1993; Hermesch et al., 2001; Logar et al., 1999). However, sustainable pig production also in SHL requires breeding attempts on improved functionality and longevity. Genetic parameters for longevity traits can alter, depending on parity. In consequence, Tholen et al. (1996) introduced different stayability definitions considering sow survival from parity 1 to 2, parity 1 to 3 and parity 1 to 4 as different traits.

Inferior feet and leg quality, and skeletal muscle damage explained up to 37% of involuntary cullings of potential breeding sows in Germany (Glodek, 1988; Schulze et al., 1998). Larsen et al. (2000) and Burrin (2001) identified nutrient and mineral supply deficiency as primary reasons for feet and leg instability with ongoing disposals, caused by genetic dispositions. Several authors (e.g., Brandt & Henne, 2004; Serenius & Stalder, 2004) suggested indirect early selection strategies on improved leg health based on type trait scoring in pigs, stimulating the implementation of a linear scoring system for functional type traits in SHL sows. Accordingly, Brandt and Henne (2004) developed a linear 9-point scoring system for conformation traits including criteria of legs, pasterns, claws, body length, body height and muscling of gilts, and they highlighted the close correlation between hind leg positions and stayability.

Some studies indicated associations between conformation traits with female fertility, e.g., the detrimental effects of leg weakness and abnormal leg conformation (Le et al., 2015). Conformation traits were also related with meat and carcass traits. Scholz et al. (2004) and Lopez-Serrano et al. (2000) reported that an increased muscle building ability contributes to leg disorders and impaired leg quality. In Landrace pigs, genetic correlations between stayability with back fat thickness and with daily gain ranged between 0.11 and 0.27, and between −0.06 and −0.32, respectively (Lopez-Serrano et al., 2000).

Especially in the small SHL purebred pig population with a closed breeding program and with a strong focus on intra-herd sow replacements in organic weaner production systems, stayability of sows is an overriding breeding goal (Klein et al., 2018). Hence, a detailed analysis of proper early indicator traits is imperative. Consequently, the aim of the present study was to implement a linear conformation trait scoring system for SHL gilts, to

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estimate respective genetic parameters, and to correlate type traits with performance, reproduction and stayability traits genetically and phenotypically.

2 | MATERIALS AND METHODS

2.1 | Herd and pedigree structure

Sow trait recording of 6042 SHL gilts considered 19 piglet-producing herds located in the German federal state of Baden-Württemberg during a 10-years period from 2010 to 2019. The sows were kept in small-scaled family farms with herd sizes in the range from 11 to 65 sows, and with a strong focus on organic farming or on alternative production systems implying access to pasture or outdoor areas.

The pedigree dataset of the sows with phenotypic records included 108,073 related animals born between 1988 and 2019. At average, 45 different SHL boars were used as sires per year. The average inbreeding coefficient for the gilts increased from 5.7% in 2010 to 9.2% in 2019. The average effective population size based on the increase of inbreeding for males and females was 42. The pedigree completeness index according to MacCluer et al. (1983) increased from 90.1% for the gilts recorded in 2010 to 100% for the gilts recorded in 2019. The average generation interval comprised 2.3 years. In genetic analyses, the gilts with records could be traced back for at least 3 generations.

2.2 | Gilt conformation and performance traits

The linear conformation trait scoring included body length (BLEN), body height (BHEI), hind leg angularity (HLANG), hind leg pastern (HLPAS), hind cannon bone strength (HCBS), hind leg position (HLPOS), front leg position (FLPOS), claw length (CLEN) and muscling (MUSC) from the 6042 SHL gilts before first insemination at the age of 180–200 days. Three trained classifier from the SHL breeding organization accomplished the type trait scoring in the 10-years period in the 19 piglet-producing herds. In this regard, a rotation system of classifiers across herds was implemented. Such research design allows the separation from herd and classifier effects. However, in previous fixed effect analyses, the classifier effect was non-significant ($p > 0.05$), and therefore not considered in ongoing genetic statistical modelling approaches. The explanation is the organized conformation trait scoring of classifiers in narrow intervals, implying a high degree of between-observer agreements and similar trait score variations for all three classifiers. For linear conformation trait scoring, a 9-point scale with increments of one point, was used. The linear conformation trait-scoring scheme with respective biological explanations is introduced in Table 1. Hence, from a breeding and husbandry perspective, the intermediate score 5 was favourable. Only for HCBS, score 9 was the optimal value. The distribution of assigned conformation trait scores is given in Figure 1. Performance traits of the classified gilts included average daily gain (ADG) from birth until the date of conformation trait scoring, and back fat thickness (BF) measured by ultrasound at the conformation trait scoring day. The mean value for DG was 510.33 g (SD = 62 g), and the mean value for BF was 14.25 mm (SD = 3.07 mm).

2.3 | Sow reproduction and stayability traits

From the same sows, reproduction traits were the number of piglets born alive (NBA) and the number of piglets weaned (NWEAN) from first, second and third farrowing. The mean value for NBA was 11.93 piglets (SD = 2.61 piglets), and the mean value for NWEAN was 10.70 piglets (SD = 2.04 piglets). Stayability was defined according to Tholen et al. (1996), i.e., the probability to survive from parity 1 to parity 2 (STAY_12), the probability to survive from parity 1 to parity 3 (STAY_13) and the probability to survive from parity 1 to parity 4 (STAY_14). Hence, stayability was a binary trait with scores 0 (= failure) or 1 (= survived). The proportion of first-litter sows with a stayability of 100% at the second parity (score = 1 for STAY_12) was 88.35%, at the third parity (score = 1 for STAY_13) was 70.01%, and at the fourth parity (score = 1 for STAY_14) was 49.99%.

2.4 | Estimation of genetic parameters

For the estimation of genetic parameters for conformation traits, NBA, NWEAN, ADG and BF, linear single-trait animal models were defined. In this regard, restricted maximum likelihood as implemented in the ASReml software package (Gilmour et al., 1998), was applied. The statistical model 1 for ADG, BF and conformation traits was:

$$y_{\mathrm{ijklm}} = \mu + \mathrm{herd}_i + \mathrm{year}_j + \mathrm{animal}_k + \mathrm{litter}_l + e_{\mathrm{ijklm}} \quad (1)$$

where.

y_{ijklm} = observations for conformation traits, ADG or BF of the m-th sow

μ = overall mean effect

herd_i = fixed effect of the i-th sow herd.

year_j = fixed effect of the j-th year for trait recording

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TABLE 1 Description of the linear conformation scheme for gilts

	Conformation trait score								
Trait	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
BLEN	Very short	Short	Slightly short	Average (−)	Average	Average (+)	Slightly long	Long	Very long
BHEI	Very small	Small	Slightly small	Average (−)	Average	Average (+)	Slightly big	Tall	Very tall
HLANG	Very angled	Angled	Slightly angled	Tendency angled	Optimal angle	Tendency steep	Slightly steep	Steep	Very steep
HLPAS	Very weak	Weak	Slightly weak	Slightly soft	Dry	Very dry	Slightly stiff	Stiff	Very stiff
HCBS	Very thin	Thin	Slightly thin	Average (−)	Average	Average (+)	Slightly strong	Strong	Very strong
HLPOS	Baker-legged	Baker-legged (−)	Out-ward	Lightly outward	Parallel	Lightly inward	Slightly inward (+)	Inward	Strong inward
FLPOS	Bow-legged	Bow-legged (−)	Out-ward	Lightly outward	Parallel	Lightly inward	Slightly inward (+)	Inward	Strong inward
CLEN	Heavy shortened outer claw	Shortened outer claw	Slightly shortened outer claw	Tendency of shortened outer claw	Even claws	Tendency of shortens inner claw	Slightly shortened inner claw	Shortened inner claw	Heavy shortened inner claw
MUSC	Very slim	Slim	Slightly slim	Average (−)	Average	Average (+)	Slightly wide	Wide	Very wide

Note: − or + indicate tendencies.

Abbreviations: BLEN, body length; BEHEI, body height; CLEN, claw length; FLPOS, front leg position; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; HLPOS, hind leg position; MUSC, muscling.

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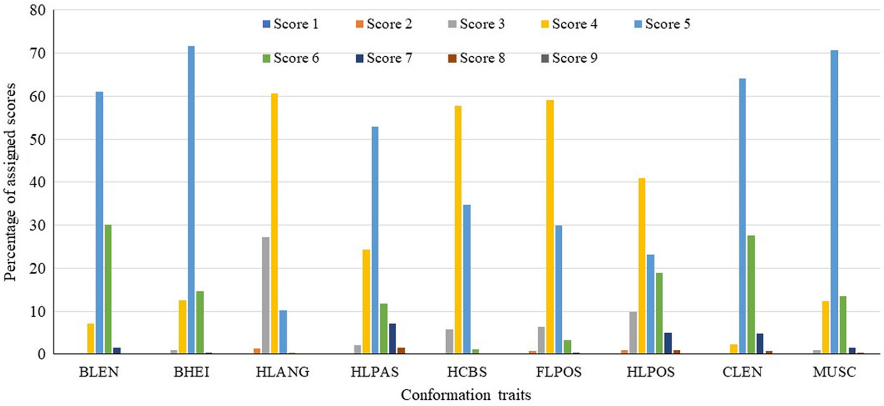

FIGURE 1 Distribution of linear conformation trait scores. BLEN, body length; BEHEI, body height; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; FLPOS, front leg position; HLPOS, hind leg position; CLEN, claw length; MUSC, muscling [Colour figure can be viewed at wileyonlinelibrary.com]

animal_k = random additive-genetic effect of the k-th animal in the pedigree

litter_l = random effect of the l-th litter.

e_{ijklm} = random residual effect

The linear single-trait animal model 2 for the reproduction traits NBA and NWEAN was:

$$y_{\text{ijklmn}} = \mu + \text{herd}_i + \text{yseas}_j + \text{parity}_k + \text{animal}_l + \text{pe}_m + \text{boar}_n + e_{\text{ijklmn}} \quad (2)$$

where

y_{ijklmn} = observations for NBA or NWEAN of the m-th sow.

μ = overall mean effect

herd_i = fixed effect of the i-th sow herd.

yseas_j = fixed effect of the j-th year-season at farrowing

parity_k = fixed effect of the k-th parity.

animal_l = random additive-genetic effect of the l-th animal in the pedigree

pe_m = random permanent effect of the m-th sow

boar_n = random effect of the n-th service sire boar.

e_{ijklmn} = random residual effect

For the binary stayability traits, a threshold single-trait animal model was applied. The corresponding statistical model 3 considering a logit-link function in ASReml (Gilmour et al., 1998) was defined as follows:

$$\text{logit}(\pi_{\text{rst}}) = \log\left[\frac{\pi_{\text{rst}}}{1-\pi_{\text{rst}}}\right] = \eta_{\text{rst}} = \varphi + \gamma_r + \lambda_s + \tau_t \quad (3)$$

π_{rst} = probability for survival of sow t from parity 1 to parity 2, 3 or 4.

φ = overall mean effect.

γ_r = fixed effect of the r-th herd.

λ_s = fixed effect of the s-th year-season of first farrowing.

τ_t = random additive-genetic effect of the t-th animal.

Heritabilities for stayability traits from model 3 were calculated using the variance of the logit link function. This implies a correction of the residual variance by factor $\pi^2/3$ (Southey et al., 2003).

Genetic correlations were estimated in bivariate runs for all trait combinations with confirmation traits considering the respective trait model 1, 2 or 3. The (co)variance matrix for random effects in the multiple-trait models including the conformation traits, ADG and BF from model 1 for a trait *1* and a trait *2* was:

$$\text{var}\begin{bmatrix} \text{animal}_1 \\ \text{animal}_2 \\ \text{litter}_1 \\ \text{litter}_2 \\ e_1 \\ e_2 \end{bmatrix} \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 & 0 & 0 \\ 0 & 0 & l_{11} & l_{12} & 0 & 0 \\ 0 & 0 & l_{21} & l_{22} & 0 & 0 \\ 0 & 0 & 0 & 0 & r_{12} & r_{12} \\ 0 & 0 & 0 & 0 & r_{12} & r_{22} \end{bmatrix}$$

where g_{11} = additive-genetic effect for trait *1*, $g_{12} = g_{21}$ = additive-genetic covariance between both traits, g_{22} = additive-genetic effect for trait *1*, l_{ij} = respective variances and covariances for the litter effects, r_{ij} = respective variances and covariances for the residual effects, and A = pedigree based relationship matrix.

The (co)variance matrix for random effects in the multiple-trait models including the conformation traits (traits *1*) from model 1 and the reproduction traits NBA and NWEAN (traits *2*) from model 2 was as follows:

$$\begin{bmatrix} \text{animal}_1 \\ \text{animal}_2 \\ \text{litter}_1 \\ \text{boar}_2 \\ \text{pe}_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 & 0 & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & I\sigma^2_{\text{litter}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & I\sigma^2_{\text{boar}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I\sigma^2_{\text{pe}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & r_{11} & r_{12} \\ 0 & 0 & 0 & 0 & 0 & r_{12} & r_{22} \end{bmatrix}$$

with I = and identity matrix, σ^2_{litter} = the variance for the litter effect, σ^2_{boar} = the variance of the service sire boar effect, σ^2_{pe}= the variance for the permanent environment, and remaining effects as stated above.

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The (co)variance matrix for random effects in the multiple-trait models including the conformation traits (traits *1*) from model 1 and the stayability traits (traits *1*) from model 3 was:

$$\operatorname{var}\begin{bmatrix}\text{animal}_1\\ \text{animal}_2\\ \text{litter}_1\\ e_1\\ e_2\end{bmatrix}\begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 & 0 & 0\\ g_{21}A & g_{22}A & 0 & 0 & 0 & 0\\ 0 & 0 & I\sigma^2_{\text{litter}} & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & r_{12} & r_{12}\\ 0 & 0 & 0 & 0 & r_{12} & r_{22}\end{bmatrix}$$

with elements as specified above.

3 | RESULTS AND DISCUSSION

3.1 | Distribution of linear conformation scores

The distribution of the assigned conformation scores as outlined in Figure 1 almost reflects a Gaussian distribution. The majority of the scores ranged between 4 and 6, slightly lopsided towards score 4. The linear type traits with best conformation quality due to a large percentage of records within the favourable intermediate score class 5 were BLEN (61.0%), BHEI (71.6%), CLEN (64.1%) and MUSC (70.7%). The traits with the lowest percentages for the optimal score assessment of score 5 were HLANG (10.2%) and HLPOS (23.1%). With regard to HCBS, the most favourable score 9 was completely missing. For HCBS, 57.8% of all records were assigned to score 4, indicating the inferior bone strength in the SHL population. For the remaining feet and leg traits, a large fraction of records in the intermediate and favourable score class 5 indicates the high quality for functional conformation traits in the SHL population. On the other hand, one could argue that classifiers do not fully use the available 9-point scale for type trait scoring. Nevertheless, the three classifiers were trained by the SHL breeding organization in close intervals, aiming on harmonized conformation trait recording and advised to utilize the broad score range. Optimal for high quality subjective type trait recording, also from the perspective of unbiased genetic evaluations, is only one trained classifier (Kristensen et al., 2006). However, in larger herdbook populations as in SHL pigs with 70 participating herds, only one person cannot handle the tremendous workload. Alternatively, the SHL breeding organization elaborated a rotation system for the three classifiers across herds, to prevent confounding between classifier and herd effects (Norman et al., 1983).

In all species pigs, dairy cattle, beef cattle, sheep and horses, a low percentage of records was observed in extreme score categories for subjectively assigned type trait or behaviour scores (e.g., Haberland et al., 2012; Hoppe et al., 2010). Hence, observers are hesitant to assign extreme values, also in justified cases, but phenotypic trait variation is imperative to infer genetic differences and to realize selection response (Schierenbeck et al., 2011), and to estimate reliable genetic covariances with other breeding goal traits (Tarrés et al., 2005). In genomic analyses for conformation traits in Danish pig breeds, Le et al. (2017) considered a three-point scale for front leg quality, back quality and hind leg quality, and a five-point scale for overall conformation. However, due to the limited number of records at the extreme ends of the linear scale, observations from these categories were merged before conducting the genetic studies. For a practical herd application, i.e., scoring by the herd owner, a 4-point scale might be favourable as indicated by Klein (2019) for litter quality traits. In contrast, for ongoing genetic evaluations reflecting the biology of a type trait, a detailed 9-point scale is suggested and used in dairy cattle breeding since decades (e.g., Gengler et al., 1999), but it is imperative to train the classifiers for utilization of the given trait range.

3.2 | Variance components and heritabilities for conformation, performance, reproduction and stayability traits

The genetic parameters for the linear conformation traits, ADG and BF are given in Table 2. The largest heritabilities were estimated for the performance traits ADG (0.22) and for BF (0.25) recorded at the conformation trait scoring date. Even larger heritabilities for ADG and BF were estimated by Mrode and Kennedy (1993) and McLaren et al. (1992) with values in the range from 0.40 and 0.60. The larger BF heritabilties were estimated when measuring backfat thickness on the carcass, but in the present study, BF was measured by ultrasound. Considering the same animals, Biermann et al. (2015) estimated a heritability of 0.48 for carcass BF and a heritability of 0.17 for ultrasound BF, which is very close to the BF heritability in the present study. Selection on BF was a major objective in the SHL population during past decades, implying a decline in phenotypic and genetic variation, possibly contributing to slightly smaller BF heritabilities than in commercial breeds. For ADG and BF, also the litter variance components were largest, possibly due to shared placental conditions affecting the foetuses metabolism and growth performance abilities (Dwyer et al., 2005). Nevertheless, the variances for the common litter effect were also moderate for the conformation traits with estimates close to the genetic variance of the respective trait. The comparable large litter variation

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TABLE 2 Variance components (σ^2_a = additive genetic variance, σ^2_{litter} = common litter variance, σ^2_e = residual variance), heritabilities with respective standard errors (se) and repeatabilities for conformation traits, ADG and BF at the conformation recording date

	Genetic parameters				
Trait	σ^2_a	σ^2_{litter}	σ^2_e	h^2 (se)	**Repeatablity**
ADG	525.63	616.91	1301.42	0.22 (0.04)	0.47
BF	1.45	1.41	3.04	0.25 (0.04)	0.48
BLEN	0.08	0.07	0.24	0.21 (0.01)	0.38
BHEI	0.07	0.06	0.22	0.20 (0.01)	0.37
HLANG	0.08	0.05	0.34	0.17 (0.02)	0.28
HLPAS	0.12	0.07	0.78	0.12 (0.03)	0.20
HCBS	0.06	0.04	0.27	0.16 (0.04)	0.27
HLPOS	0.20	0.19	1.00	0.14 (0.03)	0.28
FLPOS	0.04	0.03	0.45	0.08 (0.03)	0.13
CLEN	0.03	0.07	0.38	0.06 (0.03)	0.21
MUSC	0.04	0.06	0.29	0.10 (0.03)	0.26

Abbreviations: ADG, daily gain; BF, back fat thickness; BLEN, body length; BEHEI, body height; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; HLPOS, hind leg position; FLPOS, front leg position; CLEN, claw length; MUSC, muscling.

might be due to the statistical modelling approach and the neglected seasonal effect for trait recording. We excluded the season effect from the genetic statistical model, because this effect was not significant for conformation traits in previous fixed effect analyses. Furthermore, we attempted to increase the number of observations for contemporary groups, because of the generally small herd sizes in the SHL population. Herold et al. (2021) recently showed the importance of the contemporary group size on accuracies of genetic evaluations. Repeatabilities for objectively measured ADG and BF were larger (0.47 and 0.48, respectively) than for the subjectively recorded conformation traits. In this regard, Rydhmer (2000) indicated the quite large residual variance components for trait scores based on subjective observer impressions, implying a repeatability decline. In a similar context, Faure (1994) emphasized that subjective trait scores are frequently not Gaussian distributed, causing biased variance components. Nevertheless, linear conformation trait scores reflect the biology of a trait expression and body morphology (e.g., Doyle et al., 2020), instead of arbitrarily chosen notes.

Heritabilities were smallest for the conformation traits FLPOS (0.08) and CLEN (0.06). The linear conformation traits with the largest heritabilities were BLEN (0.20) and BHEI (0.18). Johnson and Nugent (2003) estimated moderate heritabilities for morphometric traits in pigs including body length and a body mass index in the range from 0.26 to 0.32. The slightly larger heritabilities might be due to the data basis with real length measurements instead of subjective scores. Accordingly, quite large heritabilities for morphometric traits associated with conformation which exceeded the respective estimates from subjective scoring were presented by Vanvanhossou et al. (2020) when modelling genomic relationship matrices.

Variance components and heritabilities for stayability traits and for the reproduction traits NBA and NWEAN are given in Table 3. Heritabilities slightly decreased with increasing parity, with 0.08 for STAY_12, 0.07 for STAY_13 and 0.05 for STAY_14. Similar trends, i.e., a decline of additive-genetic variances and heritabilities for survival traits with an increasing number of culled animals in late parities, was found by Shabalina et al. (2019) in dairy cows. Generally, the heritabilities for stayability traits in the present study reflect the estimates by Tholen et al. (1996) in Australian Landrace and Large White pig populations. More recently, Poulsen et al. (2020) studied stayability in commercial and multiplier herds keeping Landrace or Yorkshire sows. Heritability estimates for their stayability definition (i.e., stayability to service after first parity) reflecting STAY_12 in the present study, were substantially larger in multiplier (0.21 for Landrace, 0.29 for Yorkshire) than in commercial herds (0.02 for Landrace, 0.01 for Yorkshire). Furthermore, the only moderate genetic correlations between stayability recorded either in commercial or in multiplier herds (Poulsen et al., 2020) indicate necessary modifications in trait recording schemes and in selection index definitions. In contrast to the different herd types as considered by Poulsen et al. (2020), all SHL herds included in our study represent the same herdbook status with an identical breeding system and focus on an intra-herd replacement scheme based on their own purebred gilts (Klein et al., 2018). Hence, there is no necessity to evaluate possible genotype by environment interactions due to genetic parameter differences in different herd types.

The heritability for NBA was 0.10, and 0.08 for NWEAN, reflecting estimates in other Landrace or Large White populations (Camargo et al., 2020; Wolf et al., 2008). Putz et al. (2015) focussed on alternative litter size definitions

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TABLE 3 Variance components (σ^{a}_{a} = additive genetic variance, σ^{a}_{boar} = sire of service sire variance, σ^{a}_{pe} = permanent environmental variance of the sow, σ^{a}_{e} = residual variance) and heritabilities[a] with respective standard errors (se) for stayability and reproduction traits

	Genetic parameters				
Trait[b]	σ^{a}_{a}	σ^{a}_{boar}	σ^{a}_{pe}	σ^{a}_{e}	h^{a} (se)
Stay_12	0.29	–	–	0.31	0.08 (0.03)
Stay_13	0.25	–	–	0.21	0.07 (0.02)
Stay_14	0.19	–	–	0.20	0.05 (0.03)
NBA	0.60	0.09	0.36	5.05	0.10 (0.02)
NWEAN	0.48	0.08	0.22	5.60	0.08 (0.01)

[a] Heritabilities of the stayability traits from the logistic model are corrected according to Southey et al. (2003).

[b] STAY_12 = the probability to survive from parity 1 to parity 2,
STAY_13 = the probability to survive from parity 1 to parity 3,
STAY_14 = the probability to survive from parity 1 to parity 4,
NBA = number of piglets born alive, NWEAN = number of piglets weaned.

at different ages in both breeds Landrace and Large White. However, for all litter size traits, the heritability was close to 0.10. In the present study, the mating boar variance for NBA and NWEAN only explained 1.5% and 1.3% of the total variance, respectively. Zhang et al. (2016) reported similar small service boar effects on litter size traits in Large White sows. Consequently, the service boar variance was ignored in several modelling approaches for litter size traits (e.g., Biermann et al., 2014). The permanent environmental variance of the sow for NBA and NWEAN explained 5.9% and 3.4% of the total variance, respectively. Very similar variance ratios were reported by Putz et al. (2015), also indicating slightly decreasing permanent environmental variances with increasing piglet aging. Hence, effects of the sow might play a decreasing role for traits reflecting the individuality of piglets, such as NWEAN, piglet survival or piglet body weights (Aikins-Wilson et al., 2021). Furthermore, disturbing effects of piglet cross fostering might bias variance components with piglet aging (Alves et al., 2018), but such common practice in commercial populations is of limited relevance in the mostly organic SHL production systems.

3.3 | Correlations among linear conformation traits

The genetic and phenotypic correlations among linear conformation traits, ADG and BF are given in Table 4. Generally, genetic correlations for all trait combinations were extremer than the respective phenotypic correlations. As expected, the performance trait ADG was genetically closely related with conformation traits from the body composite, i.e., with BLEN (0.60), BHEI (0.40) and MUSC (0.50). Furthermore, the genetic correlations between the leg conformation traits HLPAS and CLEN with ADG were positive (0.27 and 0.38, respectively), indicating desired ADG for gilts with a leg score deviating from the intermediate optimum. Cannon bone strength was favourably correlated with ADG ($r_g = 0.27$, $r_p = 0.17$). According to estimates in the German local pig breed “Bunte Bentheimer”, BF was genetically positively correlated with MUSC (0.51). The genetic correlations between BF with HLPAS and FLPOS were negative (−0.24 and −0.26, respectively), indicating the tendency for increasing back fat of sows with weak pastern and bow-legged front leg positions, respectively. The remaining genetic correlations between performance traits ADG and BF with conformation traits were in a narrow range and close to zero (−0.10 to 0.08), indicating correlated genetic gain in ADG when selecting gilts with intermediate conformation trait scores.

Among all confirmation trait combinations, the strongest genetic correlations were estimated between the body size traits BLEN and BHEI (0.92) (indicating that BLEN and BHEI are genetically same trait), and between BLEN and MUSC (−0.60). Accordingly, in Duroc pigs, the strongest genetic correlation (0.87) was estimated between body length and height at withers (Ohnishia & Satoh, 2018). The SNP-based genetic correlation between body length and body height considering whole-genome sequence data was 0.63 in Large White pigs. Genomically, Hong et al. (2021) identified similar pattern for SNP marker effects for body length and body weight in Large White pigs. The moderate negative phenotypic correlations between MUSC and BLEN (−0.33), and between MUSC and BHEI (−0.35), indicate that longer and taller gilts are less muscled than normal sized pigs from the same weight class. Accordingly, Doeschl-Wilson et al. (2005) used visual image analysis for living pigs and found strongly negative associations between body size and carcass muscle dimensions.

With regard to feet and leg traits, BHEI was genetically positively correlated with HLANG (0.38, indicating steeper legs for taller gilts), and negatively correlated with FLPOS (−0.37, indicating bow-legged positions for taller gilts). The genetic correlation between HLANG with HCBS was positive (0.57), indicating that breeding on improved cannon bone strength is associated with steeper legs. Accordingly, the quite strong positive phenotypic correlation between HLANG and HCBS (0.32) reflect the practical observations made by classifiers, i.e., that a step

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TABLE 4 Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among conformation traits, ADG and BF

	Traits										
	ADG	BF	BLEN	BHEI	HLANG	HLPAS	HCBS	HLPOS	FLPOS	CLEN	MUSC
ADG		0.18 (0.12)	0.60 (0.10)	0.40 (0.09)	0.10 (0.12)	0.27 (0.05)	0.27 (0.04)	−0.04 (0.13)	−0.05 (0.09)	0.38 (0.11)	0.50 (0.10)
BF	0.14		−0.04(0.10)	−0.10 (0.11)	0.03 (0.11)	−0.24 (0.12)	−0.02 (0.12)	−0.02 (0.12)	−0.26 (0.07)	0.08 (0.07)	0.51 (0.14)
BLEN	0.47	−0.06		0.92 (0.04)	−0.02 (0.05)	−0.05 (0.07)	−0.02 (0.07)	−0.06 (0.06)	−0.29 (0.11)	0.13 (0.10)	−0.60 (0.11)
BHEI	0.38	−0.07	0.65		0.38 (0.12)	0.00 (0.09)	0.18 (0.11)	−0.06 (0.10)	−0.37 (0.11)	0.17 (0.11)	−0.57 (0.10)
HLANG	−0.02	−0.03	0.07	0.12		−0.06 (0.05)	0.57 (0.12)	−0.13 (0.05)	−0.27 (0.11)	−0.23 (0.08)	0.10 (0.10)
HLPAS	0.11	−0.09	0.04	0.04	0.01		0.10 (0.12)	0.20 (0.11)	0.38 (0.07)	0.27 (0.10)	0.36 (0.11)
HCBS	0.17	−0.01	0.04	0.03	0.32	0.10		0.31 (0.12)	−0.15 (0.10)	−0.24 (0.09)	0.40 (0.07)
HLPOS	0.01	0.01	−0.02	−0.03	0.07	0.04	0.06		0.55 (0.10)	0.17 (0.08)	0.24 (0.06)
FLPOS	−0.02	−0.07	0.02	0.03	0.07	0.02	0.04	0.14		0.15 (0.08)	−0.09 (0.12)
CLEN	0.10	0.01	0.06	0.03	−0.05	0.10	−0.07	0.04	−0.02		0.06 (0.06)
MUSC	0.31	0.24	−0.33	−0.35	−0.01	0.05	0.19	0.09	−0.02	0.01	

Abbreviations: ADG, daily gain; BF, back fat thickness; BLEN, body length; BEHEI, body height; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; HLPOS, hind leg position; FLPOS, front leg position; CLEN, claw length; MUSC, muscling.

angulation of the hind leg implied pronounced cannon bone strength (Klein, 2019). HLANG was genetically negatively correlated with the remaining feet and leg traits HLPOS (−0.13), FLPOS (−0.27) and CLEN (−0.23), indicating baker-legged positions (HLPOS), bow-legged positons (FLPOS) and shorten outer claws (CLEN) for gilts with steeper legs. Specific positions of front legs imply specific genetic dispositions for positions of hind legs, and vice versa, supported by the moderate genetic correlation between FLPOS and HLPOS (0.55). For example, breeding on inward positioned hind legs is associated with correlated selection response in inward positioned front legs. Accordingly, in genome-wide associations, Le et al. (2017) identified very similar pattern of Manhattan plots for front leg and hind leg quality with pronounced association signals on chromosome 6. However, in detailed ongoing gene annotations, different potential candidate genes for the different leg characteristics were inferred. The overlapping results based on SNP associations, but some differences in annotated candidate genes, support the moderate genetic correlation of 0.55 between FLPOS and HLPOS from the present study. Standard errors of all genetic correlation estimates were acceptable and throughout smaller than 0.12, supporting the data quality of trait recording and pedigree depth and correctness in the SHL population as indicated by Petig (2020).

3.4 | Correlations between confirmation traits with reproduction traits

Table 5 includes the genetic and phenotypic correlations between confirmation traits with the reproduction traits NBA and NWEAN. Increased BHEI and especially BLEN of sows was associated with increased litter size genetically and phenotypically. In their review evaluating the increase of litter size in Irish sows during the past 20 years, Lawlor and Lynch (2007) identified increasing feed intake and uterine capacity as major effects, which were associated with sow body size. Klein (2019) addressed the unfavourable effects of increased sow body length on feet and leg disorders, and in further consequence, on shortened sow survival, but on increased litters. Hence, litter size can be used as an indicator for stayability (Engblom et al., 2015), but alternative selection indices favouring optimal litter sizes instead of maximal values, should be developed (e.g., Täubert & Henne, 2003). Le et al. (2015) identified the effect of leg weakness and abnormal leg conformation on impaired female fertility. Accordingly, in the present study, the genetic as well as phenotypic positive correlations between HCBS with NBA and NWEAN underline the importance of cannon bone strength. Nikkilä et al. (2013) and Knauer et al. (2011) reported low to

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moderate, but favourable associations between conformation traits with age at first farrowing, litter size and the interval from weaning to conception. On the other hand, in causality, improved feet and leg quality generally implies positive effects on longevity, but Andersson et al. (2016) reported unfavourable relationships between litter size and sow stayability. Potentially, the application of recursive models or models considering feedback responses among traits, may contribute to a deeper clarification of trait associations (Gianola & Sorensen, 2004). In the present study, apart from HCBS, the genetic correlations with litter size traits were close to zero, and the phenotypic correlations did not differ significantly from zero. These correlations close to zero indicate the value of the intermediate optimum for most of the conformation traits.

In the present study, we considered NBA, NWEAN and conformation traits from first farrowing. However, some authors estimated only moderate genetic correlations between litter sizes across parities (e.g., Alfonso et al., 1997), which might be due to the effects of selection. Consequently, genetic correlations between reproduction traits and conformation traits can differ depending on the parity number as shown by Tholen et al. (1996) for genetic relationships between reproduction and stayability traits. However, for improvements of early selection for longevity traits being fully available late in life, it is especially interesting to focus on early indicator traits.

TABLE 5 Genetic correlations (r_g) with respective standard errors in brackets as well as phenotypic correlations (r_p) between linear conformation traits and the reproduction traits "number of piglets born alive (NBA)" and "number of piglets weaned (NWEAN)"

	r_g		r_p	
Traits	**NBA**	**NWEAN**	**NBA**	**NWEAN**
ADG	−0.09 (0.10)	−0.02 (0.11)	−0.01	0.00
BF	−0.18 (0.10)	−0.05 (0.10)	−0.03	−0.01
BLEN	0.20 (0.14)	0.11 (0.09)	0.18	0.10
BHEI	0.15 (0.05)	0.19 (0.12)	0.06	0.07
HLANG	−0.10 (0.14)	−0.18 (0.14)	−0.02	−0.02
HLPAS	0.09 (0.13)	0.10 (0.11)	0.03	0.04
HCBS	0.23 (0.12)	0.15 (0.13)	0.14	0.12
HLPPOS	0.02 (0.13)	0.01 (0.08)	0.00	0.00
FLPPOS	0.14 (0.14)	0.12 (0.18)	0.01	0.01
CLEN	0.06 (0.14)	0.12 (0.18)	0.02	0.02
MUSC	0.08 (0.08)	0.17 (0.10)	0.01	0.02

Abbreviations: ADG, daily gain; BF, back fat thickness; BLEN, body length; BEHEI, body height; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; HLPOS, hind leg position; FLPOS, front leg position; CLEN, claw length; MUSC, muscling.

3.5 | Correlations between confirmation traits with stayability

The genetic and phenotypic correlations between conformation traits and stayability traits of the same sows are summarized in Table 6. The performance trait ADG considering the period until conformation trait recording was genetically not correlated with STAY_12 (−0.03).

TABLE 6 Genetic correlations (r_g) with respective standard errors in brackets as well as phenotypic correlations (r_p) between linear conformation traits and stayability traits

	r_g			r_p		
Traits	**STAY_12**	**STAY_13**	**STAY_14**	**STAY_12**	**STAY_13**	**STAY_14**
ADG	−0.03 (0.09)	−0.23 (0.10)	−0.22 (0.12)	−0.01	−0.08	−0.11
BF	0.06 (0.10)	0.31 (0.11)	0.43 (0.13)	0.06	0.21	0.22
BLEN	−0.07 (0.07)	−0.08 (0.09)	−0.53 (0.12)	−0.01	−0.05	−0.10
BHEI	−0.04 (0.03)	−0.09 (0.66)	−0.24 (0.06)	−0.04	−0.04	−0.08
HLANG	0.04 (0.06)	0.27 (0.07)	0.28 (0.14)	0.02	0.05	0.10
HLPAS	−0.09 (0.12)	−0.13 (0.13)	−0.15 (0.14)	−0.03	−0.09	−0.12
HCBS	0.07 (0.13)	0.23 (0.15)	0.11 (0.15)	0.07	0.09	0.08
HLPPOS	0.13 (0.11)	0.18 (0.15)	0.16 (0.16)	0.03	0.10	0.03
FLPPOS	0.11 (0.11)	0.11 (0.12)	0.05 (0.13)	0.05	0.03	0.02
CLEN	−0.02 (0.12)	−0.12 (0.11)	−0.13 (0.13)	−0.02	−0.08	−0.01
MUSC	−0.07 (0.16)	−0.11 (0.15)	−0.24 (0.15)	−0.05	−0.07	−0.05

Abbreviations: ADG, daily gain; BF, back fat thickness; BLEN, body length; BEHEI, body height; HLANG, hind leg angularity; HLPAS, hind leg pastern; HCBS, hind cannon bone strength; HLPOS, hind leg position; FLPOS, front leg position; CLEN, claw length; MUSC, muscling; STAY_12, the probability to survive from parity 1 to parity 2; STAY_13, the probability to survive from parity 1 to parity 3; STAY_14, the probability to survive from parity 1 to parity 4.

However, moderately unfavourable genetic correlations were estimated between ADG with STAY_13 (−0.23) and with STAY_14 (−0.22). The negative correlations support the antagonistic associations between productivity and longevity in pigs as outlined in the review by Knap (2005). Consequently, Knap (2005) suggested to include, e.g., leg quality and mortality rates as fitness indicator traits into overall selection indices. In analogy to ADG, the genetic correlation between BF and the early survival trait STAY_12 was close to zero (0.06), but moderate genetic correlation were estimated between BF with STAY_13 (0.31), and between BF with STAY_14 (0.43). Accordingly, the respective phenotypic correlations were positive (0.21 and 0.22, respectively). Thaker and Bilkei (2005) focussed on physiological explanations in this regard, and they associated larger body fat depots during the suckling with improved fitness and robustness until weaning. In most of the previous studies, piglet survival traits were correlated with back fat measurements. However, as, e.g., carried out in the selection experiment by Rosendo et al. (2007), negligible trait associations were identified. Positive genetic correlations between ultrasound back fat measurements of sows with sow fitness and sow behaviour were reported by Biermann (2015) in the local "Bunte Bentheimer" pig breed, but the estimates had quite large standard errors. Nevertheless, the positive relationships between back fat with fitness or survival traits indicate the value of old and local breeds, traditionally considering back fat in breeding and selection decisions instead only focussing on lean meat percentage.

With regard to linear body size traits, unfavourable genetic associations between BLEN and BHEI were identified with STAY_14. The respective genetic correlations were −0.53 and −0.24. The detrimental effect of large body size on longevity was proved in other farm animals genetically and phenotypically, with further consequences in breeding goal definitions (e.g., Buenger et al., 2001). Oppositely, Nikkilä et al. (2013) identified positive associations between gilt body length and gilt rib shape with sow lifetime production, survival and parity dependent stayability. Nevertheless, several authors also addressed the strong effect of housing conditions in the context of survival analyses with confirmation traits, as indicated by Brandt et al. (1999) for weaner production systems. From a husbandry perspective, it is important to note that larger animal might not fit into farrowing crates or also might require higher nutrition requirement, and if these needs are not met, they are leaving the herd. In the present study, the genetic correlations between type traits with the early sow survival indicators STAY_12 and STAY_13 were close to zero, and the respective phenotypic correlations did not differ significantly from zero. These correlations close to zero indicate the value of intermediate scores for the type traits with intermediate optimum. From a statistical point of view, it should be noted that binary stayability definitions were used in phenotypic correlation analyses, implying possible biased results. For genetic analyses, linear-linear bivariate models were applied. In the context of categorical recorded confirmation traits, Vinson and Kliewer (1976) made the theoretical proof that genetic correlations from either linear-linear or linear-threshold models are expected to be the same.

Positive moderate genetic correlation were estimated between HLANG with STAY_13 (0.27) and STAY_14 (0.28), indicating the favourable effect of steeper legs on sow survival. The slightly negative and genetic phenotypic correlations between HLPAS and stayability traits indicate impaired sow longevity due to steep pasterns. HLPAS is a strong indicator of overall feet and leg quality. Aasmundstad et al. (2014) defined an overall feet and leg score on a scale from 1 to 7, whereas gilts with very upright pasterns received a score of 7. In agreement with the results from the present study, the genetic correlation between the leg score and stayability (binary definition if a sow was culled after first parity or not) was negative with −0.12. The correlations between HLPOS and FLPOS with STAY_12, STAY_13 and STAY_14 were positive, but close to zero, again supporting the intermediate optima of front and hind leg positions. Nikkilä et al. (2013) reported small and non-significant genetic correlations between leg conformation traits recorded in gilts (e.g. claw size and knee characteristics) with sow longevity. Regarding MUSC, the genetic correlation with STAY_14 was −0.24, indicating the unfavourable effects of body strength on longevity as outlined above for BHEI and BLEN.

The genetic correlations mostly close to zero with stayabiltiy indicate the importance of intermediate values for the traits with intermediate optima. However, for traits with intermediate optima, the development of alternative approaches to combine breeding values into overall breeding indices, is imperative. Conformation traits have no direct economic value, but their inclusion into overall selection indices for longevity will contribute to economy in weaner as well as in fattening pig production systems (Matthes, 2004).

4 | CONCLUSION

The distribution of scores from the 9-point linear conformation trait recording scheme as implemented for SHL gilt classifying indicate a lack of representation of records in the extreme categories and a large fraction of records allocated to the intermediate optima. A similar distribution was also observed for HCBS, the only feet and leg trait with an optimal value of 9. Hence, an explanation for the

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generally small feet and leg trait heritabilities in the range from 0.06 to 0.17 might be due to the constrained phenotypic variation. Moderate heritabilties were estimated for linear conformation traits reflecting body morphology, i.e., for BHEI (0.21) and BLEN (BLEN), implying the largest reliabilities for BHEI and BLEN among all conformation traits. Interestingly, the common litter environment explained up to 17% of the phenotypic conformation trait variation. Genetic and especially phenotypic correlations between linear conformation traits with the reproduction traits NBA and NWEAN were close to zero. Heritabilities for stayability traits considering sow survival in parities 1, 2 and 3 were quite small in the range from 0.05 to 0.08, indicating that improvement of stayability should be completed by management strategies targeted to improve environmental conditions. However, the standardized estimated breeding values (mean = 100, SD = 20) in the range from 75 to 131 indicate sufficient genetic variation for selection. For most of the conformation traits with intermediate optimum, genetic correlations with STAY were close to zero, indicating improved longevity for gilts representing the population average with scores 4, 5 or 6, and suggesting the development of appropriate selection indices in this regard.

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CONFLICTS OF INTERESTS

We declare that we have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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