





Genetic study of litter size and litter uniformity in Landrace pigs

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ABSTRACT - We aimed to estimate litter size and litter uniformity genetic parameters and genetic trends of Landrace pigs at birth and at three weeks by using multitrait analyses for 2,787 litters. The following litter traits were evaluated: number of piglets born alive (NBA), within-litter weight mean at birth (MBW), within-litter weight standard deviation at birth (SDB), within-litter weight coefficient of variation at birth (CVB), number of piglets at three weeks (NT), within-litter weight mean at three weeks (MT), within-litter weight standard deviation at three weeks (SDT), and within-litter weight coefficient of variation at three weeks (CVT). Heritability estimates for NBA, MBW, SDB, and CVB were 0.09 ± 0.04 , 0.31 ± 0.08 , 0.01 ± 0.04 , and 0.07 ± 0.05 , respectively, greater than those obtained at three weeks (0.06 ± 0.04 , 0.10 ± 0.06 , 0.01 ± 0.04 , and 0.02 ± 0.04 for NT, MT, SDT, and CVT, respectively). The genetic correlations between NBA and MBW and between MBW and CVB (-0.73 ± 0.20 and -0.93 ± 0.21 , respectively) were of moderate to high magnitudes, as well as the genetic correlations between CVT and SDT (0.85 ± 0.39). Genetic correlations between MBW and MT, SDB and SDT, CVB and CVT, and NBA and NT were 0.73 ± 0.16 , 0.69 ± 0.54 , 0.36 ± 0.80 , and 0.95 ± 0.06 , respectively. The genetic trends were linear for NBA and CVB and quadratic for MBW and SDB, whereas for all traits at three weeks, they were close to zero. Within-litter weight coefficient of variation (CV) may be the most appropriate variation measure for application in breeding programs, especially at birth, due to its greater heritability estimate and high and negative genetic correlation with MBW. The genetic trends show that NT does not follow the increase in NBA, emphasizing the need to review the breeding goals.

Keywords: coefficient of variation, genetic parameters, genetic trends, piglet, variation

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Introduction

Litter size at birth and weaning are among the reproductive traits of greatest economic impact on pig production profitability. Traditionally, pig breeding programs have focused on improving litter size (Chen et al., 2019); however, increased litter size may affect litter uniformity, which is another trait of great importance on pig production efficiency (Deen, 2002; Sell-Kubiak et al., 2015). High within-litter weight variation may be associated with low piglet survival rates, since litters with low uniformity present a greater number of piglets with low birth weight. Such piglets have low level of body energetic store and impairment of both colostrum intake and access to function and productive teats (Milligan et al., 2002b; Quiniou et al., 2002; Zhang et al., 2016). In the integrated production systems widespread

in Brazil, piglets may be refused by the companies or the pig producer earns lower remuneration when their weights are outside the ideal range recommended for the different growth stages.

Achieving optimal litter uniformity at birth is still a challenge in production systems, since the measurement of the individual piglet weight at birth may be laborious, and only the average or total litter weights are usually recorded. However, reducing the litter variation at birth is of great importance, since uniform litters at birth remain uniform until slaughter (Fix, 2010) and reduce the need of litter equalization, known as cross-fostering, which has great operational cost and is questionable from a sanitary point of view. In addition, uniform litters enable the all-in/all-out management (Zindove et al., 2013; Wang et al., 2016), essential for the maintenance of appropriate sanitary conditions on the farm.

Variation within litters is usually measured by the standard deviation (SD) or the coefficient of variation (CV) expressed relative to the average litter weight at a specific time (Damgaard et al., 2003; Wolf et al., 2008; Zhang et al., 2016). The efficiency of a selection program for these traits will depend on knowledge of their genetic (co)variance structure and genetic progress over the years. In this context, the estimation of genetic parameters and genetic trends for litter size and within-litter uniformity in different production phases becomes crucial, benefiting all the production system. Therefore, we aimed to estimate litter size and litter uniformity genetic parameters and genetic trends of Landrace pigs at birth and at three weeks.

Material and Methods

Pre-existing databases were used in the analyses; therefore, no approval on the Ethics Committee was required.

Data of 2,787 litters (34,790 piglets) from 893 Landrace sows of first to eighth parity orders were recorded on farms located in Paraná State, southern Brazil (longitude 49°45'18.10" W, latitude 24°12'52.00" S, and elevation of 961 m above sea level), from January 2009 to April 2016.

The following litter traits were evaluated: number of piglets born alive (NBA), within-litter weight mean at birth (MBW), within-litter weight standard deviation at birth (SDB), within-litter weight coefficient of variation at birth (CVB), number of piglets at three weeks (NT), within-litter weight mean at three weeks (MT), within-litter weight standard deviation at three weeks (SDT), and within-litter weight coefficient of variation at three weeks (CVT).

For traits evaluated at three weeks, the weights were pre-adjusted to 21 days, as follows:

$$WT = \{[(WW - BW)/WA] \times 21\} + BW;$$

in which WT is the piglet weight adjusted to 21 days of age, WW is the piglet weight at weaning, BW is the piglet weight at birth, and WA is the piglet age at weaning.

The within-litter weight SD and CV at birth and at three weeks were calculated for the variation traits. The CVB and CVT, expressed in percentage (%), were calculated as follows:

$$CVB (\%) = [(SDB/MBW) \times 100];$$

$$CVT (\%) = [(SDT/MT) \times 100];$$

wherein CVB and CVT are the within-litter weight CV at birth and at three weeks, respectively; SDB and SDT are the within-litter weight SD at birth and at three weeks, respectively; and MBW and MT are the within-litter weight mean at birth and at three weeks, respectively.

The reduction in the within-litter weight CV from 18.38 (6.58) at birth to 9.52 (7.50) at three weeks (Table 1) may have occurred due to cross-fostering, which consists of standardizing the weight and number of piglets according to the sow capacity. Most of the evaluated litters came from gilts ($n = 891$), and litter size ranged from 5 to 20 piglets at birth, with almost 80% of data coming from litters with 9 to 16 piglets (Table 2).

Table 1 - Descriptive statistics of litter traits in Landrace pigs

Trait (unit)	N ¹	Average ²	SD	Min ³	Max ⁴
NBA (piglets)	2,787	12.48	3.24	5.00	20.00
MBW (kg)	2,787	1.48	0.23	0.70	2.49
SDB (kg)	2,787	0.26	0.09	0.01	0.63
CVB (%)	2,787	18.38	6.58	0.70	48.73
NT (piglets)	2,787	11.38	3.07	5.00	20.00
MT (kg)	2,787	6.14	0.76	3.51	9.86
SDT (kg)	2,787	0.58	0.46	0.00	2.20
CVT (%)	2,787	9.52	7.50	0.07	36.47

NBA - number of piglets born alive; MBW - within-litter weight mean at birth; SDB - within-litter weight standard deviation at birth; CVB - within-litter weight coefficient of variation at birth; NT - number of piglets at three weeks; MT - within-litter weight mean at three weeks; SDT - within-litter weight standard deviation at three weeks; CVT - within-litter weight coefficient of variation at three weeks; SD - standard deviation.

¹ Number of observations.

² Average values of litter traits.

³ Minimum trait value.

⁴ Maximum trait value.

Table 2 - Number of litters analyzed according to sow parity order and litter size at birth

Parity order	Number of litters
1	891
2	681
3	481
4	319
5	204
≥6	211
Litter size at birth	
≤8	340
9-10	390
11-12	658
13-14	659
15-16	453
≥17	287

Litters with 5 to 20 NBA or NT and contemporary groups (CG) with more than 10 sows were considered in the analyses. The CG was composed by herd (farms 1, 2, or 3), year (2009 to 2016), and season of birth (1 - January to March, 2 - April to June; 3 - July to September, 4 - October to December). The complete pedigree file had a total of 1,267 animals, 124 sires, and 349 dams over five generations.

The genetic connectedness among CG was assessed using the AMC software (Roso and Schenkel, 2006), based on the total number of direct genetic links between CG due to the number of common offspring of boars and/or sows. Ten direct genetic links were required as minimum to include a CG in the set of connected CG. In total, 71 CG were included in the connectedness analysis.

Genetic parameters were estimated by multitrait analyses (4×4) at birth for NBA, MBW, SDB, and CVB and at three weeks for NT, MT, SDT, and CVT using a repeatability animal model in ASReml software (Gilmour et al., 2009). In addition, genetic correlations between NBA and NT, MBW and MT, SDB and SDT, and CVB and CVT were estimated by bivariate analyses.

The analyses were performed by applying the following model:

$$y = X\beta + Z_1a + Z_2s + Z_3p + \varepsilon,$$

wherein y is the vector of observations; β is the vector of fixed effects (CG) and linear and quadratic effects of the covariate parity order; a is the vector of direct additive genetic effects; s is the vector of paternal genetic effects; p is the vector of permanent environmental effects; ε is the vector of random residual effects; X , Z_1 , Z_2 , and Z_3 are the incidence matrices of fixed, direct additive genetic, paternal genetic, and permanent environmental effects, respectively.

It was assumed that $a \sim N(0, A \otimes G)$, $s \sim N(0, A \otimes S)$, $p \sim N(0, I \otimes P)$, and $e \sim N(0, I \otimes R)$; \otimes is the direct product operator; G , S , P , and R are the covariance matrices for the direct additive genetic, paternal genetic, permanent environmental, and residual effects, respectively; A is the pedigree-based relationship matrix; and I is an identity matrix.

Genetic trends were obtained by the linear or quadratic regression of the average of estimated breeding values for males and females on birth year, weighted by the number of observations.

Results

The connectedness analysis revealed a percentage of CG connectedness of 100%, i.e., no contemporary groups or animals were found disconnected.

The additive genetic variances ranged from 0.00007 to 2.69300 for traits at birth, with the minimum additive genetic variance for SDB and the maximum additive genetic variance for CVB (Table 3). At three

Table 3 - Estimates of (co)variance components from multitrait models for litter traits at birth

Trait	NBA	MBW	SDB	CVB
Additive genetic (co)variance				
NBA	0.89910			
MBW	-0.08355	0.01461		
SDB	-0.00018	-0.00009	0.00007	
CVB	0.99580	-0.18380	0.00630	2.69300
Permanent environmental (co)variance				
NBA	0.14080			
MBW	0.00043	0.00509		
SDB	0.00025	0.00125	0.00044	
CVB	-0.04144	0.01841	0.01437	0.84370
Paternal genetic (co)variance				
NBA	0.13900			
MBW	-0.00620	0.00161		
SDB	-0.00040	0.00032	0.00009	
CVB	0.04243	0.00250	0.00230	0.12540
Residual (co)variance				
NBA	8.83400			
MBW	-0.15230	0.02614		
SDB	0.02385	-0.00227	0.00586	
CVB	3.65600	-0.47270	0.42250	35.2400
Phenotypic (co)variance				
NBA	10.01200			
MBW	-0.24159	0.04745		
SDB	0.02352	-0.00079	0.00646	
CVB	4.65230	-0.63559	0.44544	38.90200

NBA - number of piglets born alive; MBW - within-litter weight mean at birth; SDB - within-litter weight standard deviation at birth; CVB - within-litter weight coefficient of variation at birth.

weeks, the additive genetic variances ranged from 0.00068 to 0.52980, with the minimum variance for SDT and the maximum variance for NT (Table 4).

Heritabilities ranged from 0.01 to 0.31 for traits evaluated at birth and from 0.01 to 0.10 for traits evaluated at three weeks. In general, traits measured at birth presented greater heritability estimates when compared with traits evaluated at three weeks (Tables 5 and 6).

Table 4 - Estimates of (co)variance components from multitrait models for litter traits at three weeks

Trait	NT	MT	SDT	CVT
Additive genetic (co)variance				
NT	0.52980			
MT	-0.14620	0.05574		
SDT	0.00867	-0.00336	0.00068	
CVT	0.36110	-0.13520	0.01454	0.43210
Permanent environmental (co)variance				
NT	0.25690			
MT	0.08590	0.03102		
SDT	0.03278	0.00960	0.00531	
CVT	0.41100	0.11480	0.07140	0.99870
Paternal genetic (co)variance				
NT	0.07209			
MT	-0.00895	0.00277		
SDT	0.00691	-0.00100	0.00102	
CVT	0.13740	-0.02134	0.01937	0.37540
Residual (co)variance				
NT	7.90400			
MT	-0.15440	0.44400		
SDT	0.04661	-0.00574	0.07982	
CVT	0.91990	-0.74560	1.30200	23.08000
Phenotypic (co)variance				
NT	8.76260			
MT	-0.22363	0.53353		
SDT	0.00950	-0.00049	0.08682	
CVT	1.82930	-0.78736	1.40730	24.88800

NT - number of piglets at three weeks; MT - within-litter weight mean at three weeks; SDT - within-litter weight standard deviation at three weeks; CVT - within-litter weight coefficient of variation at three weeks.

Table 5 - Heritability estimates ± standard errors (†, diagonal), genetic (below diagonal), and phenotypic (above diagonal) correlations obtained from multitrait model for litter traits at birth

Trait	NBA	MBW	SDB	CVB
NBA	0.09±0.04†	-0.35±0.03	0.09±0.03	0.24±0.03
MBW	-0.73±0.20	0.31±0.08†	-0.04±0.034	-0.47±0.03
SDB	-0.02±0.96	-0.09±0.75	0.01±0.04†	0.89±0.01
CVB	0.64±0.34	-0.93±0.21	0.45±0.66	0.07±0.05†

NBA - number of piglets born alive; MBW - within-litter weight mean at birth; SDB - within-litter weight standard deviation at birth; CVB - within-litter weight coefficient of variation at birth.

Genetic correlations between NBA and MBW and between MBW and CVB (-0.73 ± 0.20 and -0.93 ± 0.21 , respectively) were moderate to high, whereas the other traits at birth presented low and negligible genetic correlations (Table 5). Most of the genetic correlations for traits at three weeks could not be considered different from zero considering an interval of 1.96 standard errors either side of the genetic correlation estimates, which results in a 95% confidence interval (Zuidema and Wynne, 1989). Only the genetic correlation between SDT and CVT (0.85 ± 0.39) was high and different from zero (Table 6). Genetic correlations between NBA and NT, MBW and MT, SDB and SDT, and CVB and CVT were 0.95 ± 0.06 , 0.73 ± 0.16 , 0.69 ± 0.54 , and 0.36 ± 0.80 , respectively.

The genetic trends were linear for NBA (Figure 1) and CVB (Figure 2) and quadratic for MBW (Figure 3) and SDB (Figure 4), whereas for all traits at three weeks, they were close to zero (Figures 1 to 4).

Table 6 - Heritability estimates \pm standard errors (\dagger , diagonal), genetic (below diagonal), and phenotypic (above diagonal) correlations obtained from multitrait model for litter traits at three weeks

Trait	NT	MT	SDT	CVT
NT	$0.06 \pm 0.04^\dagger$	-0.10 ± 0.03	0.11 ± 0.03	0.12 ± 0.03
MT	-0.85 ± 0.45	$0.10 \pm 0.06^\dagger$	-0.00 ± 0.03	-0.22 ± 0.03
SDT	0.46 ± 1.39	-0.55 ± 1.85	$0.01 \pm 0.04^\dagger$	0.96 ± 0.00
CVT	0.75 ± 0.94	-0.87 ± 1.02	0.85 ± 0.39	$0.02 \pm 0.04^\dagger$

NT - number of piglets at three weeks; MT - within-litter weight mean at three weeks; SDT - within-litter weight standard deviation at three weeks; CVT - within-litter weight coefficient of variation at three weeks.

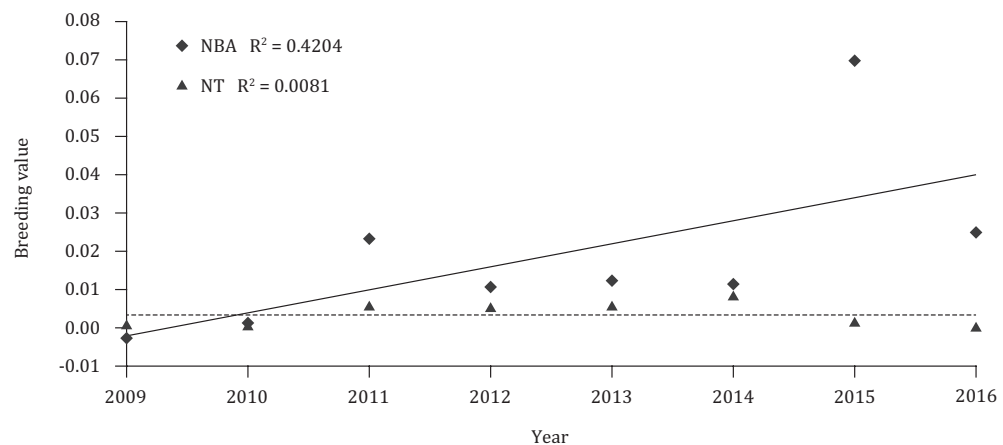


Figure 1 - Genetic trends for number of piglets born alive (NBA: $y = -12.081829897 + 0.006012733x$) and for number of piglets at three weeks (NT: $y = -0.2173564814 + 0.0001097269x$) in Landrace pigs.

Discussion

Litter size and uniformity are among the traits of greatest importance in pig production systems. The NBA has been traditionally considered in the selection goals of pig breeding programs (Högberg and Rydhmer, 2000; Zindove et al., 2014), while litter uniformity is commonly neglected (Banville et al., 2015). The reasons for the variation in the birth weight of piglets are complex and include, among others: degree of oocyte maturation, time required for ovulation, uterine capacity for implantation and placentation, position in uterine horn, uteroplacental size and efficiency in nutrient transportation, uterine and placental angiogenesis, sow nutritional status, and other genetic and epigenetic effects (Wu et al., 2006; Yuan et al., 2015). Among the dispersion measures used to describe the litter weight

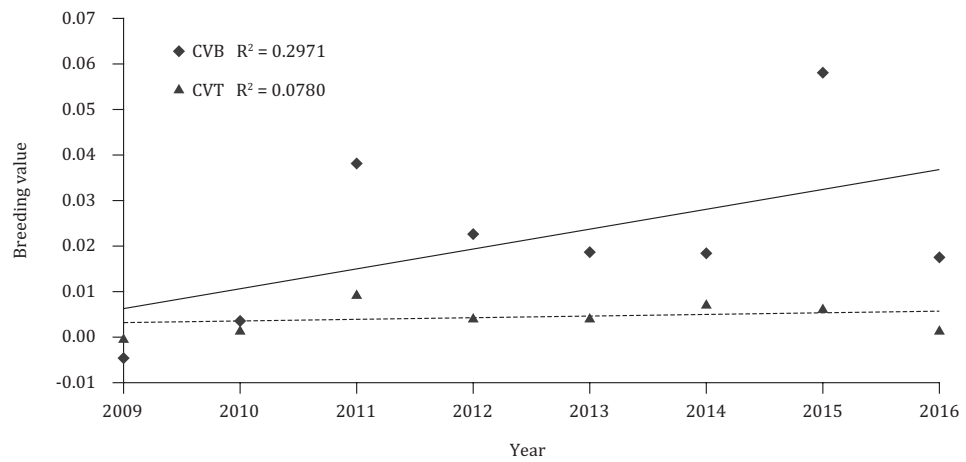


Figure 2 - Genetic trends for within-litter weight coefficient of variation at birth (CVB: $y = -8.73681352 + 0.00435192x$) and for within-litter weight coefficient of variation at three weeks (CVT: $y = -0.745251708 + 0.000372422x$) in Landrace pigs.

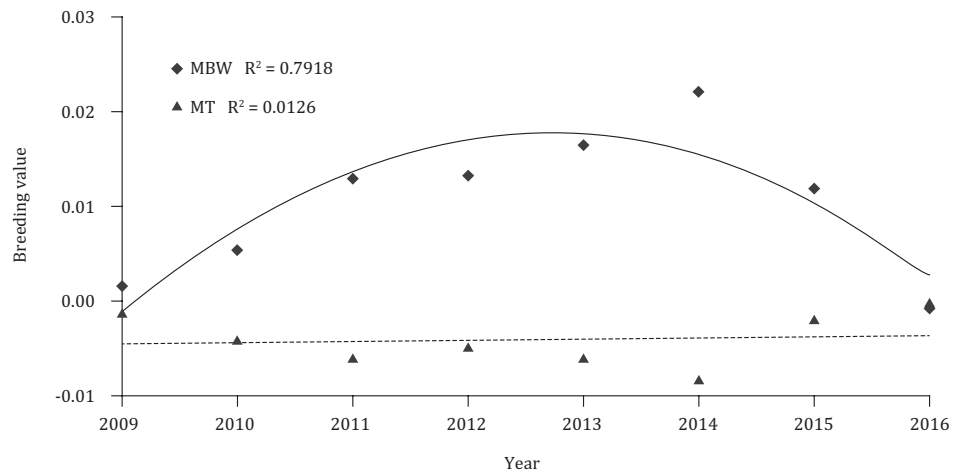


Figure 3 - Genetic trends for within-litter weight mean at birth (MBW: $y = -5570.121 + 5.534981x - 0.001375011x^2$; maximum point: 2012.7) and for within-litter weight mean at three weeks (MT: $y = -0.256777930 + 0.000125653x$) in Landrace pigs.

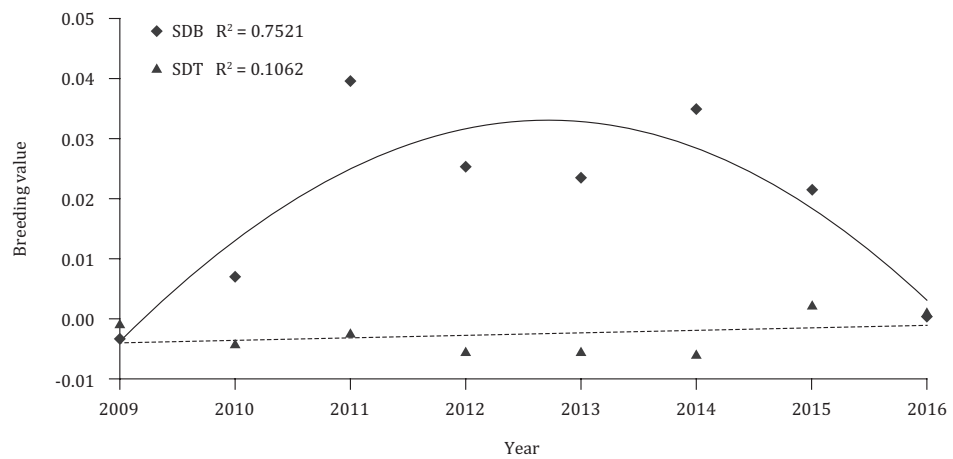


Figure 4 - Genetic trends for within-litter weight standard deviation at birth (SDB: $y = -1106384 + 10.99419x - 0.002731235x^2$; maximum point: 2012.7) and for within-litter weight standard deviation at three weeks (SDT: $y = -0.8362231511 + 0.0004142746x$) in Landrace pigs.

uniformity, the CV and/or the SD have been the most applied (Hermesch et al., 2001; Milligan et al., 2002b; Quiniou et al., 2002; Damgaard et al., 2003; Wolf et al., 2008; Canario et al., 2010; Zindove et al., 2013; Banville et al., 2015; Wang et al., 2016; Zhang et al., 2016).

Heritability estimates obtained for NBA, SDB, and CVB were low and similar or lower than those reported in literature (Roehe, 1999; Högberg and Rydhmer, 2000; Hermesch et al., 2001; Wolf et al., 2008; Canario et al., 2010; Banville et al., 2015; Lázaro et al., 2015). Roehe (1999) estimated heritability of 0.08 ± 0.04 for NBA in 14,950 pigs. Högberg and Rydhmer (2000) and Banville et al. (2015) reported heritability estimates of 0.09 ± 0.03 and 0.19 ± 0.04 for NBA in Yorkshire sows and in a composite Chinese dam line, respectively. Lázaro et al. (2015) compared statistical models with different polynomial degrees and homogeneous and heterogeneous residual variance structures to evaluate the genetic trajectories of litter size in pigs. These authors estimated heritabilities ranging from 0.04 to 0.29 for NBA in Landrace pigs. Canario et al. (2010) estimated heritabilities of 0.11 ± 0.02 and 0.10 ± 0.05 for NBA and SDB, respectively, for a Norwegian Landrace nucleus population. Wolf et al. (2008) reported heritabilities of 0.14 ± 0.020 , 0.03 ± 0.009 , and 0.05 ± 0.011 for NBA, SDB, and CVB, respectively, in a hyperprolific pig line. Hermesch et al. (2001) reported heritabilities of 0.11 ± 0.03 for CVB in commercial pig lines. In our study, CVB presented higher heritability compared with SDB (0.07 ± 0.05 and 0.01 ± 0.04 , respectively), which is desirable for selection strategies.

The heritability value for MBW was moderate and similar to the values reported by Canario et al. (2010) (0.32 ± 0.06) and Varona et al. (2007) (0.24 ± 0.06). On the other hand, the estimate was higher than that reported by Wolf et al. (2008) (0.16 ± 0.020) and lower than that reported by Banville et al. (2015) (0.51 ± 0.06). The moderate heritability found for MBW in the present study shows that genetic improvement for this trait by selection might be feasible.

The heritability estimates at three weeks were lower compared with estimates at birth and with those reported in literature (Högberg and Rydhmer, 2000; Damgaard et al., 2003; Canario et al., 2010; Banville et al., 2015; Zhang et al., 2016). Högberg and Rydhmer (2000) estimated heritabilities of 0.13 ± 0.03 and 0.30 ± 0.04 for NT and MT, respectively, in Yorkshire sows. Canario et al. (2010) estimated heritabilities of 0.17 ± 0.02 and 0.08 ± 0.01 for MT and SDT, respectively, in a Norwegian Landrace nucleus population. Damgaard et al. (2003) reported heritability of 0.06 ± 0.03 for SDT, while Banville et al. (2015) found higher heritability for the same trait (0.15 ± 0.05). Zhang et al. (2016) reported heritability of 0.07 ± 0.03 for CVT, which was higher than the CVT heritability reported in the present study (0.02 ± 0.04).

In a review addressing the sow nutritional impact on the within-litter variation of piglets' weight, Yuan et al. (2015) considered that the genetic influences on litter homogeneity in pigs could be verified by the genetic correlations among the analyzed traits. According to Hermesch et al. (2001), the MBW should be considered in pig breeding programs to avoid increased mortality rates due to larger litter sizes. Several studies have been performed aiming to increase survival rates in pigs; however, this trait showed a negative genetic correlation (-0.73 ± 0.20) with NBA, also confirmed in the studies performed by Wolf et al. (2008) and Banville et al. (2015), in which genetic correlations of -0.39 ± 0.09 and -0.60 ± 0.09 , respectively, were reported between NBA and MBW. This result is unfavorable, since the traditional selection for increased NBA would be decreasing the MBW as a correlated response and, consequently, decreasing litter uniformity, since the genetic correlation between MBW and CVB was high and negative (-0.93 ± 0.21).

Genetic correlations between NBA and SDB or CVB were low and not different from zero (-0.02 ± 0.96 and 0.64 ± 0.34 , respectively), which indicates that selection for hyperprolificity would have no influence on within-litter weight variation at birth. Banville et al. (2015) also reported negligible genetic correlation between NBA and SDB (0.17 ± 0.17), while Wolf et al. (2008) reported low to moderate genetic correlations between NBA and SDB or CVB (0.17 ± 0.14 and 0.38 ± 0.11 , respectively). On the other hand, genetic correlation between MBW and CVB (-0.93 ± 0.21) was high and favorable, indicating that selection strategies focused on increased MBW would decrease within-litter weight variation. This result was different from the genetic correlation estimated between MBW and

CVB reported by Hermesch et al. (2001) (-0.26 ± 0.12). The other traits at birth presented low and negligible genetic correlations, which is in agreement with the results of Canario et al. (2010).

Most of the genetic correlations for traits at three weeks were negligible, except for the high and positive genetic correlation between SDT and CVT (0.85 ± 0.39). Therefore, it is not recommended to simultaneously use these traits in a selection index. Högberg and Rydhmer (2000), Banville et al. (2015), and Damgaard et al. (2003) also estimated negligible genetic correlations between NT and MT (-0.03 ± 0.14), NT and SDT (-0.35 ± 0.25), and MT and SDT (0.22 ± 0.25), respectively. On the other hand, Canario et al. (2010) estimated high and positive genetic correlation between MT and SDT (0.77 ± 0.27).

Regarding the genetic correlations between traits at birth and at three weeks, only NBA and NT and MBW and MT presented moderate to high and positive correlations (0.95 ± 0.06 and 0.73 ± 0.16 , respectively), which was favorable, since selection for greater NBA would increase NT, as well as greater MBW would present a positive correlated response on MT. Genetic correlation between NBA and NT was higher than those reported by Banville et al. (2015) (0.39 ± 0.19) and Su et al. (2007) (0.72 ± 0.06). Direct selection for NT is usually impaired due to cross-fostering, which also makes it difficult to adequately estimate genetic parameters for this trait (Su et al., 2007). Therefore, based on the high genetic correlations between NBA and NT estimated in this study, improvement of NT can be achieved by selecting for NBA. Regarding the genetic correlation between MBW and MT, Damgaard et al. (2003) also reported moderate estimates (0.61 ± 0.09) for Swedish Yorkshire sows, indicating that selection for higher MBW may increase MT as well. Canario et al. (2010) used multitrait models to evaluate combinations of MBW, MT, SDB, and SDT and also reported moderate genetic correlations between MBW and MT (0.60 ± 0.16). Banville et al. (2015) estimated a correlation of 0.71 ± 0.09 between these traits, similar to the result of the present study. In this way, a simple breeding strategy would be the selection for greater MBW with a correlated response on MT, without impairing the uniformity, since MBW showed moderate heritability (0.31 ± 0.08) and favorable genetic correlations with CVB (-0.93 ± 0.21) and MT (0.73 ± 0.16).

The genetic correlations between the variation traits at birth and at three weeks were not different from zero (0.69 ± 0.54 and 0.36 ± 0.80 between SDB and SDT and CVB and CVT, respectively), which was different from the results of Damgaard et al. (2003), Canario et al. (2010), and Banville et al. (2015), who reported moderate to high genetic correlations between SDB and SDT (0.71 ± 0.21 , 0.51 ± 0.31 , and 0.53 ± 0.17 , respectively). Different statistical models, amount of data, and pig breeds evaluated may explain some differences in genetic parameter estimates for traits at birth and at three weeks compared with those reported in the literature.

The genetic trend analysis is a useful tool for assessing genetic changes over the years (Santana Júnior et al., 2010), aiding to verify the need for adjustments in breeding programs (Euclides Filho et al., 1997). In this study, NBA and CVB showed linear and positive genetic trends, while the genetic trends for MBW and SDB were quadratic, increasing from the year 2009 until reaching the maximum point between 2012 and 2013, followed by a decreasing trend until 2016 (Figures 3 and 4).

Despite the low heritability estimate for NBA, its genetic trend was positive, with annual genetic gains of 0.006 piglets, lower than that observed by Chen et al. (2003), who analyzed several pig breeds and verified genetic gains of 0.018 piglets per litter per year. Pires et al. (2000) estimated greater genetic gains (0.0509 piglets) for the same trait in Landrace pigs from 1993 to 1996; however, the annual genetic gain for litter size at weaning estimated by these authors was only 0.0084.

According to Wolf et al. (2008), greater NBA may lead to greater birth weight variability, which can be compensated by cross-fostering. This practice may justify the virtually unchanged genetic gain for MT over the years. On the other hand, the quadratic effect observed for MBW showed that the selection for hyperprolificity was not followed by gains in uterine capacity, placental efficiency, and other factors influencing this trait.

The linear genetic trends found for NBA and CVB corroborate the results obtained by Wolf et al. (2008), who observed lower piglet uniformity with an increase in litter size at birth. However, the quadratic genetic trends for MBW and SDB over the years, followed by the linear genetic trends for NBA, lead us to presume that there is an optimal intermediate NBA value that provides maximum MBW, although this may be also associated with greater SDB. According to Zaleski and Hacker (1993), litters with nine piglets at birth provided lower stillbirth. On the other hand, Canario et al. (2006) observed that litters with 12 piglets showed the lowest percentage of stillborn piglets. The selection for larger litters results in a greater number of piglets with low birth weight, and the improvement of the piglet survival rates should be considered (Milligan et al., 2002a).

In this context, the development of strategies that decrease the within-litter variation at birth and other traits negatively related to piglet survival is essential for pig production feasibility (Yuan et al., 2015). The unfavorable genetic trends for MBW and CVB showed the need to review the breeding goals to evaluate the consequences of increased litter size.

All traits at three weeks showed genetic trends close to zero (Figures 1 to 4). These results were different from those of Chen et al. (2003), who verified annual genetic gains of 0.004 piglets per litter at weaning. In addition, Pires et al. (2000) and Chen et al. (2003) observed positive annual genetic gains for litter weights at birth and at 21 days in Landrace pigs (0.0232 and 0.1118 kg, respectively). The economic impact of the within-litter variation of piglet weight has not received the proper attention by the breeding companies (Wolf et al., 2008; Zindove et al., 2014), which is evidenced by the low genetic progress observed in the last years for within-litter uniformity traits at three weeks.

Conclusions

The within-litter weight coefficient of variation may be the most appropriate variation measure for application in breeding programs, especially when evaluated at birth, due to its greater heritability estimate and high and negative genetic correlation with within-litter weight mean. The genetic trends show that the number of piglets weaned does not follow the increase in the number of piglets born alive, emphasizing the need to review the breeding goals, mainly evaluating the economic losses due to the reduction of the within-litter weight mean and the increase of its coefficient of variation.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: E.G. Camargo, E.A.P. Figueiredo, F.F. Silva and P.S. Lopes. Data curation: E.G. Camargo, E.A.P. Figueiredo and P.S. Lopes. Formal analysis: D.B.D. Marques and F.F. Silva. Funding acquisition: F.F. Silva and P.S. Lopes. Investigation: E.A.P. Figueiredo, F.F. Silva and P.S. Lopes. Methodology: D.B.D. Marques, F.F. Silva and P.S. Lopes. Project administration: E.G. Camargo and P.S. Lopes. Resources: E.G. Camargo, E.A.P. Figueiredo, F.F. Silva and P.S. Lopes. Supervision: P.S. Lopes. Validation: P.S. Lopes. Visualization: D.B.D. Marques and P.S. Lopes. Writing-original draft: E.G. Camargo, D.B.D. Marques, E.A.P. Figueiredo, F.F. Silva and P.S. Lopes. Writing-review & editing: D.B.D. Marques, E.A.P. Figueiredo and P.S. Lopes.

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