

Influence of some sow characteristics on within-litter variation of piglet birth weight*

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Within-litter variation of piglet birth weight (BW0) is associated with an increased piglet mortality and a high variability in pig weight at weaning and weight or age at slaughter. Data collected in two experimental herds were used to quantify within-litter variability in BW0 and to assess the influence of factors mainly related to the sow. Within 24 h after birth, piglets born alive were individually weighed and stillborn piglets were collectively (first data set) or individually (second data set) weighed. The first data set was restricted to litters with no or only one stillborn piglet (3338 litters). It was used to assess the influence of genetic selection on BW0 variation by comparing litter characteristics before (1994 to 1996) and after (2001 to 2004) the development of hyperprolific sows in this herd. The second data set included all litters (n = 1596) from sows born between 2000 and 2004. For each litter, mean BW0 (mBW0) and its coefficient of variation (CV_{BW0}) were calculated. Then, variance analyses were performed to test the influence of litter size, parity, year of sow birth and season at conception. Prolificacy improvement was associated with an increased CV_{BW0} in litters from pure Large White (LW) and Landrace × Large White (LR × LW) crossbred sows. The CV_{BW0} averaged 21% and was significantly influenced by litter size and parity. It increased from 15% to 24% when litter size varied from less than 10 piglets to more than 15 piglets. The proportion of small piglets (i.e. weighing less than 1 kg) increased concomitantly. The CV_{BW0} was not repeatable from a parity to the following. It was lowest for first and second parities (20%) and thereafter increased progressively. The CV_{BW0} was positively related to sow's backfat thickness gain during gestation. Taking into account litter size, parity, year of sow birth and season at conception explained 20% of BW0 variation. Thus, major part of heterogeneity is due to other factors, presumably including embryo genotype, on the one hand, and factors that influence embryo and foetus development, such as epigenetic factors, on the other hand.

Keywords: birth weight, piglet, sow, within-litter variation

Introduction

At birth, littermates greatly differ in terms of weight and maturity. Within herds, a great within-litter heterogeneity of piglet birth weight (BW0) is associated with an increased mortality before weaning and a high variation in weight at weaning (English and Smith, 1975; Pettigrew *et al.*, 1986; Tuchscherer *et al.*, 2000; Milligan *et al.*, 2002). It may also have repercussions on slaughter management within batches with regard, on the one hand, to time taken to reach the most valuable carcass weight range and, on the other hand, to heterogeneity among pigs (Le Cozler *et al.*, 2004). Detrimental effects of low BW0 were also reported on meat quality (Gondret *et al.*, 2006). If consequences of BW0

heterogeneity on piglet survival and growth performance have been extensively described, factors susceptible to influence this criterion have been less investigated. Within breed, heterogeneity of BW0 has been shown to increase with litter size (Milligan *et al.*, 2002; Quiniou *et al.*, 2002). Because of the possible benefits of more homogeneous litter, the possibility of genetic improvement of within-litter variation in BW0 by selective breeding was also studied (Damgaard *et al.*, 2003). The aim of the present study was to describe the within-litter variation in piglet BW0 and to assess the influence of additional factors mainly related to the sow, such as parity, birth date and body reserves.

Material and methods

Data sets

All data have been collected on LW and LR × LW crossbred sows. The first two data sets described piglet BW0 measured

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within the 24 h after birth. Piglets were recorded as alive or stillborn. No floatation test was performed to discriminate pigs that died during the birth progress and those who were born alive but died shortly thereafter. In the third data set, piglets were weighed immediately at birth, i.e. before the first suckling. The fourth data set described foetus weights.

In the *first data set*, data were collected in the INRA experimental herd (35590 Saint-Gilles, France), from January 1994 to June 2005. From the mid-1990s, highly prolific sows (also called 'hyperprolific' sows) have been introduced in French herds, as well as in other European countries. In the INRA herd, genetic improvement of prolificacy was obtained through artificial insemination. From 1996 to 2004, semen came from selected lines of 'hyperprolific' LW and LR boars characterised by a high breeding value for litter size. This data set was used to study changes in litter characteristics before and after this genetic improvement. Initially, data included 4479 litters born from LW and LR \times LW crossbred sows. Litter ranks averaged 2.5 and 60% of litters were first and second litters. Piglets were individually weighed within the first 24 h of life, except for stillborn piglets that were weighed together. Because individual BW0 of all piglets, born alive and stillborn, are necessary to describe accurately the within-litter variation of BW0, this data set was restricted to litters with no or only one stillborn piglet (3338 litters representing 75% of all litters). Analyses compared litters from sows born between 1994 and 1996 ($n = 990$) and between 2001 and 2004 ($n = 782$).

In the *second data set*, data were collected in the experimental station of IFIP-Institut du Porc (35850 Romillé, France). Calculations were performed on 1596 litters from LR \times LW sows born between 2000 and 2004. Half litters were first or second parities. All piglets, born alive and stillborn, were weighed individually within the first 24 h after birth. During gestation, feed allowance was adapted individually for all sows to body condition at mating. Sows were weighed 7 days after conception and within 24 h after farrowing. Backfat thickness was ultrasonically measured at the P2 site 7 days after conception and at the end of gestation (105th day on average).

In the *third data set*, data were collected from LR \times LW sows in the IFIP and INRA experimental herds (111 and 120 litters, respectively). Piglets were weighed within the first 5 min after birth and identified. The actual BW0 was designated as 'BW0 at time 0' (BWt0). Piglets were also weighed at 24 h of age (BWt24).

In the *fourth data set*, data originated from an experiment performed on 43 LW pregnant gilts born in 1991 and 1992 (Père *et al.*, 1997). Gilts were slaughtered at 112 days of pregnancy. Number of alive and dead fetuses and ovulation rate were recorded and live fetuses were individually weighed.

Variables and calculations

For each litter in data sets 1 and 2, numbers of total piglets born, born alive and stillborn were recorded. Within-litter mean (mBW0), standard deviation (SD_{BW0}) and coefficient of variation (CV_{BW0}) of piglet birth weight were calculated.

Within-litter minimal and maximal BW0 were also determined. In addition, for data set 2, piglets were categorised in four classes according to their absolute BW0 (<1 kg; 1 to 1.4 kg; 1.4 to 1.8 kg; or >1.8 kg) or to the difference between their BW0 and the mBW0 of their litter. Classifications were based on the literature. Probability of pre-weaning survival is significantly reduced (below 75%) for piglets weighing less than 1 kg and is beyond 95% for piglets weighing more than 1.8 kg (Pettigrew *et al.*, 1986; Roehe and Kalm, 2000; Quiniou *et al.*, 2002). Other authors reported a greater risk of dying for piglets weighing less than 75% to 80% of the mean BW0 of the litter as reviewed by Le Dividich (1999). Accordingly, classes in the second classification corresponded to piglets weighing less than 75% of mBW0, between 75% and 100%, between 100% and 125%, or 125% and more of mBW0. For data set 3, within-litter CV of piglet weight was calculated for weight at birth (CV BWt0) and 24 h after birth (CV BWt24). For data set 4, within-litter mean and CV of living fetuses weight were calculated.

Statistical analyses

Analysis of variance was performed using the MIXED procedure (Statistical Analysis Systems Institute (SAS), 1999). All models included at least litter size, parity and sow's birth year as main factors. The random effect of sow within birth year was also included in order to take into account the permanent environment effect of the sow. Sow's birth year was chosen rather than year of farrowing because it better represented genetic selection for improved prolificacy. Litter size was categorised in five classes: less than 10 total born piglets, 10 to 11, 12 to 13, 14 to 15, 16 and more. Parity was also categorised in five classes: first, second, third and fourth, fifth and sixth, seventh and more. Effect of birth year was tested within parity. Effect of categorised litter size was tested within parity because of the correlation between these two factors ($r = 0.13$, $P < 0.001$). For the first data set, the main effects were litter size, parity, sow's birth year pooled in two periods (1994 to 1996 v. 2001 to 2004) and breed (LW v. LR \times LW). For the second data set, the main effects were litter size, parity, sow's birth year, season at conception and the interaction season \times sow's birth year. Season represented the first, second, third and fourth trimesters of the year. When an effect was significant, means were compared using the Student–Newman–Keuls test after GLM. Repeatability was calculated from variance component estimates (proc MIXED; SAS, 1999) with the parity (categorised), birth year and batch as fixed effects and sow as random one. Relationships between CV_{BW0} and criteria of sow body condition were tested using proc REG (SAS, 1999), taking also into account the litter size. Results are expressed as raw data.

Results and discussion

Influence of genetic selection for prolificacy on piglet BW0 variation

Retrospective analysis of the first data set was conducted to assess the evolution of litter characteristics over a decade.

Table 1 Descriptive statistics and analysis of variance of data collected before and after genetic improvement of sow prolificacy (from 1994 to 1996 and from 2001 to 2004) at the INRA experimental herd (data set 1)

	LW sows		LR × LW sows		Statistics (<i>P</i> values) [†]				
	94 to 96	01 to 04	94 to 96	01 to 04	r.s.d.	Period	Breed	Parity	Litter size
Litter [‡] (<i>n</i>)	767	200	223	582					
Total born (<i>n</i>)	10.6	12.4	11.5	13.1	3.1	<0.001	<0.001	<0.001	–
Born alive (<i>n</i>)	10.3	12.2	11.2	12.8	3.1	<0.001	<0.001	<0.001	–
Stillborn (<i>n</i>)	0.3	0.3	0.3	0.3	0.4	0.691	0.765	0.002	–
Individual BWO									
Mean (kg)	1.56	1.38	1.53	1.44	0.16	<0.001	<0.001	<0.001	<0.001
SD _{BWO} (kg)	0.27	0.28	0.27	0.28	0.08	0.213	0.565	<0.001	<0.001
CV _{BWO} (%)	18	21	18	20	5.9	<0.001	0.027	0.266	<0.001
Maximal BWO (kg)	1.93	1.80	1.91	1.84	0.18	0.005	0.035	<0.001	<0.001
Minimal BWO (kg)	1.09	0.9	1.04	0.92	0.26	0.003	0.075	<0.001	<0.001

r.s.d. = residual standard deviation; BWO = birth weight; CV_{BWO} = coefficient of variation of BWO.

[†]The model (proc MIXED) included period (birth year range), parity (categorised) and litter size within parity as main effects. The interactions were not significant thus they were removed from the model.

[‡]Litters with zero or only one stillborn piglet.

^{||}Average maximal and minimal BWO.

Because the occurrence of stillbirth increases with litter size (Fraser *et al.*, 1997), the exclusion of litters with at least two stillborn piglets from the analysis was likely to eliminate more large litters than small ones. Thus, average litter size in this data set (11.7 total born piglets) was lower than in the whole population of sows in the herd (12.4) and in French herds over the same period (12.6 piglets; IFIP, 1995 to 2005). Litter size was higher in LR × LW crossbred than in LW sows (12.2 v. 11.1 piglets; *P* < 0.05), which is consistent with data from the national survey (IFIP, 1995 to 2005) and can be related to a heterosis effect.

For LW sows, genetic improvement over 10 years resulted in 1.8 extra piglet per litter and a reduction by 180 g in mBWO (Table 1). Concomitantly, SD_{BWO} did not increase significantly, whereas CV_{BWO} increased by 3%. Although less marked, a similar evolution of litter characteristics was observed for LR × LW crossbred sows (Table 1). In an experiment using frozen semen of boars born in 1977 or 1998, Tribout *et al.* (2003) previously reported such an increase in CV_{BWO} related to genetic improvement over 20 years for LW sows (20% v. 18%). In their study, however, the impact of selection on the other characteristics of piglets and litter at birth differed from our present findings. Despite the increase in prolificacy, they did not observe a reduction in piglet BWO but a lower piglet maturity at birth (Canario *et al.*, 2007). Moreover, according to Tribout *et al.* (2003), the increase in CV_{BWO} over time was caused by an increase in the maximum piglet BWO and not by a higher frequency of small piglets. In the present data set, both average maximal and minimal BWO decreased as prolificacy increased. Discrepancies may originate in the experimental design or the period considered.

Within-litter variation of BWO from highly prolific sows (2000 to 2004)

Prolificacy in the second data set (14 piglets; Table 2) was higher than the average prolificacy in French herds calculated

from the database of Technical Management of Sows Herds (13.1 piglets from 2000 to 2004; IFIP, 2001 to 2005), but representative of the most performing herds in terms of prolificacy. Within-litter variation in individual BWO averaged 21%, ranged from 0% to 51% (with total born piglets ranging from 2 to 21) and was significantly influenced by litter size and sow parity.

Mean BWO decreased and variation in BWO (SD_{BWO} and CV_{BWO}) increased as litter size increased (Table 3), as previously reported (Le Dividich, 1999; Milligan *et al.*, 2002; Quiniou *et al.*, 2002). In the present herd, when litter size varied from less than 10 piglets to more than 15, mean BWO decreased by 510 g while CV_{BWO} increased from 15% to 24%. This rise in CV_{BWO} was accompanied by an increased proportion of small piglets. According to Le Dividich (1999), piglets weighing less than 75% or 80% of the mBWO in the litter can be considered as small. As most piglets weighing less than 1 kg are included in this category, they can also be considered as small. When litter size increased from 9 to 16, the proportion of small piglets weighing less than 1 kg increased from 3% to 15% (Figure 1). It remains debatable whether these small piglets have a higher risk to be stillborn but they clearly have a lower survival rate than their heavier littermates (Roehe and Kalm, 2000; Milligan *et al.*, 2002; Quiniou *et al.*, 2002). On the contrary, a high survival rate, beyond 90%, was reported when piglets weighed more than 1.4 kg at birth (Quiniou *et al.*, 2002). When piglets were categorised relatively to mBWO, the proportion of heavier piglets increased with litter size (Table 3). However, when absolute BWO was considered, the proportion of heavy piglets decreased, simultaneously with the increased proportion of small piglets (Figure 1). While most piglets weighed more than 1.4 kg at birth in small litters, they were only 50% in litters of 16 piglets and more. Such large litters represented 30% of the litters born in French herds in 2006 (IFIP, 2007). It is therefore not surprising that piglet mortality increased from

Table 2 Descriptive statistics and analysis of variance of data collected at the IFIP experimental herd (data set 2, n = 1596 litters)

	Mean ± s.e.	Analysis of variance (P values) [†]				
		r.s.d.	Litter size	Parity	Year of birth	Season
Mean parity	3.0 ± 1.9					
Total born (n)	14.0 ± 3.7	3.2	–	<0.001	0.017	0.227
Born alive (n)	13.1 ± 3.4	3.0	–	<0.001	0.015	0.408
Stillborn (n)	0.9 ± 1.3	1.3	–	<0.001	0.018	0.347
Individual BW0						
Mean (kg)	1.53 ± 0.26	0.15	<0.001	<0.001	0.001	0.049
SD _{BW0} (kg)	0.31 ± 0.10	0.09	<0.001	<0.001	0.001	0.377
CV _{BW0} (%)	21 ± 8	6	<0.001	<0.001	0.079	0.065

r.s.d. = residual standard deviation; BW0 = birth weight; CV_{BW0} = coefficient of variation of BW0.

[†]The model (proc MIXED) included litter size within parity (categorised) parity, birth year within (categorised) parity, season at conception and year × season interaction as main effects. The interaction was not statistically significant.

Table 3 Effect of litter size on piglet BW0 variation (data set 2, n = 1596 litters)

	Litter size (class)					Statistics [†]	
	≤9	10 to 11	12 to 13	14 to 15	≥16	r.s.d.	Litter size
n	195	154	276	394	579		
Mean parity	2.6	2.3	2.5	2.6	3.5		
Litter size							
Total born (n)	7.1	10.6	12.6	14.5	17.7	3.5	
Born alive (n)	6.9	10.2	12.0	13.7	16.1	3.3	
Stillborn (n)	0.3	0.4	0.6	0.8	1.5	1.3	
Mean BW0 (kg)	1.88 ^a	1.67 ^b	1.57 ^c	1.48 ^d	1.38 ^e	0.19	<0.001
SD _{BW0} (kg)	0.28 ^a	0.29 ^a	0.32 ^b	0.32 ^b	0.33 ^b	0.09	<0.001
CV _{BW0} (%)	15 ^a	18 ^b	21 ^c	22 ^c	24 ^d	6.8	<0.001
Distribution in BW0 classes (%)							
<0.75 μ	6 ^a	9 ^b	12 ^c	13 ^c	16 ^d	8	<0.001
0.75 μ to μ	39 ^a	36 ^b	34 ^{bc}	33 ^c	31 ^d	13	<0.001
μ to 1.25 μ	50 ^a	49 ^a	46 ^b	44 ^b	40 ^c	13	<0.001
>1.25 μ	5 ^a	6 ^b	9 ^c	10 ^c	13 ^d	9	<0.001

BW0 = birth weight; CV_{BW0} = coefficient of variation of BW0.

[†]Litter size effect (see statistical model in Table 2). Student–Newman–Keuls test was used to determine differences between groups after GLM. Values with different superscripts, within rows, differ significantly (P < 0.05).

12% to more than 14% over the past 10 years since the diffusion of hyperprolific sows (IFIP, 1997 to 2007).

Stillbirth was related to CV_{BW0} (r = 0.23, P < 0.001). This relationship is likely to reflect the influence of litter size, given the concomitant increase in stillbirth occurrence and CV_{BW0} with litter size (Table 3). Nevertheless, such a positive correlation, although weak (r comprised between 0.14 and 0.21), was also observed within class of litter size (data not shown), suggesting that stillbirth might be influenced by litter heterogeneity *per se*. The role of within-litter BW0 variation has been pointed out in between-breed variability of stillbirth (Canario *et al.*, 2006). Within breed also, litter heterogeneity could enhance stillbirth probability. Potential underlying mechanisms are unclear since the present study did not discriminate piglets that died during the birth process from those dying shortly thereafter. More heterogeneous litters contain more light piglets, which are more

susceptible to premature death and also, according to several authors, more susceptible to death during the birth process (Leenhouders *et al.*, 1999; Knol *et al.*, 2002; Canario *et al.*, 2006). Heterogeneous litters also contain more heavy piglets, which tend to have also a greater risk of death during farrowing (Canario *et al.*, 2006). Whether a relationship exists between litter uniformity and farrowing duration should be investigated.

Sows in first and second parities had less heterogeneous litters than older ones (Table 4), in agreement with Bolet and Etienne (1982). Piglets from primiparous sows have been reported to be more uniform than piglets from older sows, this effect being related to parity effect on litter size (Milligan *et al.*, 2002) or not (Pettigrew *et al.*, 1986). In the present study, CV_{BW0} was similar in first and second parity sows despite a difference in nearly two total born piglets on average. This would suggest that litter heterogeneity is

partly influenced by parity effect *per se*. Indeed, considering the relationship between litter size and CV_{BW0} presented in Table 3, heterogeneity of second litters seems to be in accordance with their reduced size. On the contrary, for first litters, CV_{BW0} seems rather low, since litter size averaged nearly 14 piglets (Table 4). This finding needs to be further investigated. In contrast, parity effect on CV_{BW0} was not significant in the first data set (Table 1). Such a discrepancy is likely related to the exclusion of litters with more than one stillborn piglet in data set 1. This eliminated mainly older sows, from parities five and more, since stillbirth frequency increased with sow parity (Table 4).

No significant effect of the season at conception was found on CV_{BW0} or litter size (Table 2). In contrast, in a retrospective study including 20 000 litters, Xue *et al.* (1994) reported a reduction in litter size and litter weight when conception occurred in summer. Discrepancies can be partly attributed to different climates and different sample sizes. It cannot be ruled out also that herd management (sow nutrition and housing, hormonal treatments, etc.) modulates summer effects on reproductive performance in the different herds considered (Quesnel *et al.*, 2005).

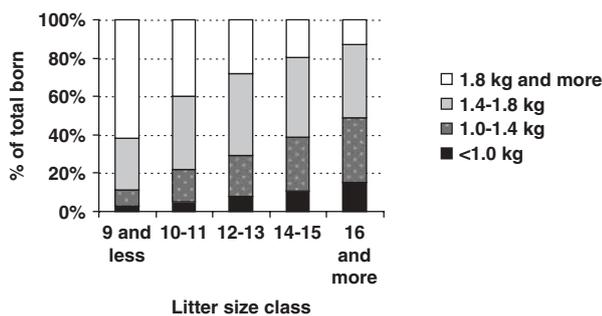


Figure 1 Effect of litter size on piglet distribution into BW0 classes (raw data from data set 2, n = 1596 litters).

Season at conception influenced mBW0 (Table 2), with piglets conceived in spring being heavier ($P < 0.1$) than piglets born in the other seasons. Consistently, piglets born in summer have been shown to be heavier ($n = 1833$ litters, Bolet and Etienne, 1982).

Influence of sow's body condition on piglet BW0 variation Significant relationships were found between sow's body condition and CV_{BW0} (Table 5). Litter heterogeneity increased with body weight (BW) at the beginning and the end of gestation. Parity partly contributed to this relationship as sow BW significantly increased with age (data not shown). Heterogeneity increased also with backfat thickness at the end of gestation. However, relationships were very weak and no longer significant when parities were considered separately. A weak negative relationship was observed between within-litter variation in piglet birth weight and sow's backfat thickness at conception. This correlation was mainly due to three to four, and seven and more parities sows (Table 5).

The CV_{BW0} was not linked with BW gain during gestation but with backfat thickness gain. In this herd, backfat gain is likely to reflect adaptation of feed allowance during gestation to body reserve mobilisation during previous lactation. Indeed, higher backfat thickness gains were obtained with lowest initial BW ($r = -0.52$, $P < 0.001$). We may wonder whether body reserve loss during lactation may influence BW0 heterogeneity in the subsequent litter. Besides sows' body condition, it has been well established that sows' metabolic status influences follicle and oocyte quality with consequences on embryo survival and development (Zak *et al.*, 1997; Quesnel *et al.*, 1998; Ferguson *et al.*, 2006), and also on within-litter variation in piglet birth weight (van den Brand *et al.*, 2006). These effects were generally attributed to specific hormones, essentially insulin and IGF-I. Large-scale studies should be conducted

Table 4 Effect of sow parity on piglet BW0 variation (data set 2, n = 1596 litters)

	Parity (class)					Statistics [†]	
	1	2	3 to 4	5 to 6	≥7	r.s.d.	Parity
Litter							
n	432	349	470	261	86		
Total born (n)	14.0 ^a	12.3 ^b	14.5 ^a	15.3 ^c	15.1 ^c	3.5	<0.001
Born alive (n)	13.2 ^a	11.7 ^b	13.5 ^{ab}	14.4 ^b	13.3 ^a	3.3	<0.001
Stillborn (n)	0.8 ^{ab}	0.6 ^a	0.9 ^b	1.3 ^c	1.8 ^d	1.3	<0.001
Mean BW0 (kg)	1.45 ^a	1.64 ^b	1.57 ^c	1.47 ^a	1.44 ^a	0.19	<0.001
SD _{BW0} (kg)	0.28 ^a	0.31 ^b	0.33 ^c	0.34 ^c	0.35 ^c	0.09	<0.001
CV _{BW0} (%)	20 ^a	20 ^a	22 ^b	24 ^c	25 ^c	6.8	<0.001
Distribution in BW0 classes (%)							
<0.75 μ	11 ^a	11 ^a	13 ^b	15 ^c	16 ^c	8	<0.001
0.75 μ to μ	36 ^a	34 ^{ab}	32 ^{bc}	31 ^c	30 ^c	13	0.013
μ to 1.25 μ	45	47	44	40	40	13	0.154
>1.25 μ	8 ^a	8 ^a	11 ^b	14 ^c	14 ^c	9	0.011

r.s.d. = residual standard deviation; BW0 = birth weight; CV_{BW0} = coefficient of variation of BW0.

[†]See statistical model in Table 2. Student–Newman–Keuls test was used to determine differences between groups after GLM. Values with different superscripts, within rows, differ significantly ($P < 0.05$).

Table 5 Relationships between coefficient of variation of birth weight (CV_{BWO}) and body condition of the sows during gestation (equation of regression with correction for litter size, data set 2)^{*,†}

Y	All parities			Slope of Y per class of parity				
	Intercept	b × LS	c × Y	1	2	3 to 4	5 to 6	≥7
Body weight (kg)								
At conception	4 ± 1	0.75 ± 0.05	0.033 ± 0.005	0.026	-0.005	0.059	0.050	0.024
P value	<0.001	<0.001	<0.001	0.38	0.87	<0.001	0.06	0.65
After farrowing	1 ± 1	0.77 ± 0.05	0.035 ± 0.005	0.016	-0.028	0.077	0.069	0.050
P value	0.26	<0.001	<0.001	0.44	0.28	<0.001	0.01	0.40
Variation [‡]	10 ± 1	0.80 ± 0.05	-0.016 ± 0.015	0.016	-0.028	0.077	0.069	0.050
P value	<0.001	<0.001	0.28	0.44	0.28	<0.001	<0.001	0.40
Backfat (mm)								
At conception	12 ± 1	0.84 ± 0.05	-0.16 ± 0.06	-0.11	-0.05	-0.24	-0.14	-0.49
P value	<0.001	<0.001	0.004	0.30	0.74	0.02	0.21	0.01
Before farrowing	7 ± 1	0.82 ± 0.05	1.15 ± 0.06	0.09	-0.03	0.11	0.03	0.35
P value	<0.001	<0.001	0.01	0.45	0.86	0.29	0.82	0.21
Variation [‡]	8.0 ± 0.7	0.85 ± 0.05	0.32 ± 0.06	0.20	0.03	0.48	0.15	0.64
P value	<0.001	<0.001	<0.001	0.08	0.85	<0.001	0.16	<0.001

[‡]Number of observations: 1519 for body weight; 1585 for backfat thickness.

^{*}Equation used for regression: $CV_{BWO} = \text{intercept} + b \times LS + c \times Y$ with Y as by condition parameter and LS = litter size. Values are mean ± s.e.

[‡]Variation: weight after farrowing minus weight at conception or backfat thickness before farrowing minus backfat thickness at conception.

to relate sows' metabolic status before ovulation and subsequent CV_{BWO} .

Repeatability of mean BWO and within-litter BWO variation

Estimates of repeatability for litter size were similar to those previously reported (Le Cozler *et al.*, 1997; Damgaard *et al.*, 2003; Nguyen *et al.*, 2006). Values of repeatability for CV_{BWO} were similar in both herds. They were relatively low, indicating that CV_{BWO} was not a repeatable criterion in successive litters (Table 6). Similarly low values were found for SD_{BWO} . This is consistent with findings from Damgaard *et al.* (2003) reporting low repeatability (0.17) for within-litter s.d. in birth weight. Repeatability for mean BWO was much stronger, as previously described (Damgaard *et al.*, 2003; Nguyen *et al.*, 2006). Repeatability for maximal BWO was also found to be strong, whereas repeatability for minimal BWO was low. The maximal weight is likely limited by morphological and physiological constraints related to the sow. Consistent with these observations, CV_{BWO} was, in both herds, highly correlated with minimal BWO ($r = -0.82$, $P < 0.001$, $n = 1596$ litters) but not with maximal BWO ($r = -0.02$, $P > 0.1$).

Other causes for the high variability of BWO variation

Findings presented above pointed out the high variability of within-litter BWO variation, with CV_{BWO} varying from a few per cent up to 50%. Taking into account the effects of litter size, sow parity, sow's birth year and season at conception explained less than one-fourth of the variation in CV_{BWO} (Table 2).

Piglet weighing procedure. As usually in experimental herds, piglets in the present studies were weighed within 24 h after birth, with some litters being weighed shortly

Table 6 Values of repeatability of litter performance (data sets 1 and 2)

Herd	IFIP		INRA [†]	
	LR × LW	LR × LW	LR × LW	LW
Sows				
Sows (n)	1065	816		740
Total born	0.20	0.17		0.17
Born alive	0.18	0.13		0.15
Stillborn	0.14	0.11		0.07
Individual BWO				
Mean	0.42	0.37		0.33
SD_{BWO}	0.14	0.14		0.12
CV_{BWO}	0.12	0.15		0.10
Maximal BWO [‡]	0.48	0.42		0.39
Minimal BWO [‡]	0.16	0.19		0.14

BWO = birth weight; CV_{BWO} = coefficient of variation of BWO.

[†]Repeatability was calculated on all litters for piglet numbers and on litters with no or only one stillborn for other criteria.

[‡]Average maximal and minimal BWO.

after birth and others later. Then, in some litters, competition for teats may have exacerbated differences in weight and vitality among piglets. However, from data collected immediately at birth and 24 h later precisely on same piglets, it appears that increase in BWO variation between birth and 24 h of age is limited (+0.5% in the first herd and +2% in the second one; Table 7). Therefore, variability in weighing time after birth seems to participate only marginally in CV_{BWO} variability.

In utero litter size. The existing literature (Milligan *et al.*, 2002; Quiniou *et al.*, 2002) and our findings indicated that CV_{BWO} clearly depends on litter size at birth but that litter size explained only a small part of this variation. Litter size effect partly reflects *in utero* competition for nutrients between foetuses during foetal growth and development.

Table 7 Variation in piglet weight recorded at various times after birth in litters born from crossbred LR × LW sows (data set 3)

Herd	Year of farrowing	Weighing at birth and 24 h later [†]				Weighing within 24 h [†]		
		n	Litter size	CV BWt0 [†]	CV BWt24 [†]	n	Litter size	CV BW0 [†]
INRA	2002 to 2005	120	13.7	20	20	737	12.9	20 [*]
IFIP	2004 to 2005	111	14.8	20	22	426	14.0	23

BW0 = birth weight; CV_{BW0} = coefficient of variation of BW0; CV: coefficient of variation (%).

[†]Piglet weights were recorded within 5 min after birth (BWt0) and 24 h later, precisely (BWt24), or once within 24 h after birth (BW0).

^{*}Calculated from litters with zero or one stillborn piglet.

Table 8 Relationship between ovulation rate and litter characteristics during late gestation, in LW gilts (Pearson's coefficients, n = 43, data set 4)

	No. foetuses [†]	No. living foetuses	Mean weight [†]	CV weight [†]
Ovulation rate	0.36	0.30	-0.11	0.36
P value	0.02	0.05	0.48	0.02
Foetuses		0.83	-0.26	0.31
P value		< 0.001	0.09	0.04
Living foetuses			-0.34	0.38
P value			0.03	0.01

[†]Number of foetuses, alive and dead, present in the uterus at 112 days of gestation; mean weight of living foetuses; coefficient of variation of foetus weight.

In moderately prolific sows, i.e. having ovulation rate that did not exceed 20 or 22, litter size has been shown to be related to ovulation rate and to the number of developing conceptuses (King and Williams, 1984; Blasco *et al.*, 1996). In this context of moderate prolificacy, variation in foetus weight in late gestation was correlated to the number of living foetuses and to ovulation rate (Table 8). In hyperprolific sows, however, ovulation rate and number of developing embryos largely exceed the number of piglets at birth (Vonnahme *et al.*, 2002). Besides, heterogeneity is already evident between embryos at the end of the first month of gestation. In hyperprolific LW gilts, CV of embryo weight averaged 9% around 33 days of gestation (Martinat-Botté and Quesnel, unpublished data). In addition, within-litter distribution of weight has been shown to be established as soon as 30 or 35 days of gestation (van der Lende *et al.*, 1990; Wise *et al.*, 1997; Finch *et al.*, 2002). It can therefore be hypothesised that events occurring during the first month of gestation play a key role in CV_{BW0} variation. As mentioned above, 'events' such as nutrition and metabolic status even before ovulation are also susceptible to influence embryo development, and consequently CV_{BW0}. However, no difference in CV_{BW0} was reported by Quiniou and Quesnel (2008) between sows fed 1.7 or 2.6 times their maintenance requirement during the first month of gestation but fed the same amount of feed over the whole gestation.

Conclusion

Selection for prolificacy over the past decades has been associated with a deterioration of within-litter variation in piglet BW0. It increases significantly with litter size and

parity. Nevertheless, taking into account litter size, parity, sow birth date and season at conception explains less than one-fourth of BW0 variation. Variation in BW0 was significantly but weakly correlated to backfat thickness gain during gestation. In addition, this criterion is not repeatable from one parity to the next. Thus, a major part of heterogeneity is due to other factors not identified in the present investigations. It can be assumed that these factors include embryo genotype on the one hand, and factors that influence embryo and foetus development, such as epigenetic factors, on the other hand.

Recently, a canalising selection experiment on within-litter variability of BW0 in rabbits had a favourable selection response on birth weight variability and positive consequences for the young survival (Garreau *et al.*, 2004). In pigs, considering the lack of identified environmental factors allowing the breeders to reduce BW0 variability, and that genetic improvement of BW0 variability by selective breeding seems possible (Damgaard *et al.*, 2003), selection on BW0 uniformity would be a relevant approach to improve piglet survival.

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