CHAPTER 4

ESTIMATION OF HETEROSIS AND INBREEDING

4.1. Introduction

The animal breeder has two main tools for changing animals genetically - selection and crossbreeding-. Pig producers have been using crossbreeding as an effective way of improving reproductive performance for decades. The mean phenotypes of progeny from crosses between populations often differ from the average of the parents, a phenomenon known as heterosis. This improvement associated with heterosis or hybrid vigour, comes from an increase in heterozygosity, which leads to better than average genotypic values at dominant loci (Rothschild and Bidanel, 1998).

Mating animals of different breeds produces crossbred progeny that will express heterosis in different ways. Individual heterosis will influence performance (survivability, early growth) as a result of animals themselves being crossbred. Maternal heterosis will influence reproductive and fitness traits as well as maternal ability that would lead to enhanced offspring performance as a result of the dam being crossbred (Simm, 1998).

A related phenomenon called inbreeding depression arises within populations. Inbreeding is the mating of two related animals. Inbred individuals almost always have a reduced mean phenotypic value of characters connected with reproductive capacity or physiological efficiency compared with progeny of non related animals. This decline in fitness associated with inbreeding, comes from an increase in homozygosity within populations with the consequent decrease in heterozygosity.

In species like pigs with extensive parental care, if maternal performance (the ability to raise young) is adversely affected by inbreeding, then a purebred individual's phenotype will be influenced not only by its own level of inbreeding but also by its mother (Lynch and Walsh, 1998).

Current crossbreeding systems implemented in commercial piggeries worldwide generally consist of three- or four-way crossbreeding systems. The aim of three-way crossbreeding systems is to take full advantage of maternal and individual heterosis. In order to achieve these, commercial piggeries need to breed first cross (F1) females, which will have high additive genetic merit for reproduction and associated characteristics and will fully express maternal heterosis. These F1 females will be mated to boars from a specialized and unrelated Terminal Sire Line (TSL), which will have high additive genetic merit for growth, feed efficiency, leanness and carcass traits. The crossbreeding of the F1 hybrid female with a TSL boar will take full advantage of the reproductive capabilities of the sow and the growth and carcass characteristics of the boar. In Australia these F1 breeding females are commonly produced by crossbreeding two specialized maternal lines such as Large White and Landrace. TSL boars are often purebred Duroc.

Three-way cross systems are divided in two stages, the first consists of crossbreeding two maternal lines in a multiplier herd for producing F1 hybrid gilts. Secondly, these gilts will be delivered to the commercial piggeries jointly with the TSL boars, in order to crossbreed them. This type of system creates a challenge when estimating heterosis. As already mentioned, heterosis is the extra performance presented by the progeny compared with the average of their parents. In order to estimate heterosis the performance of the parents and their progeny has to be recorded under the same conditions. Comparing parents and progeny raised under completely different environments will neglect the environmental effects and could over- or under-estimate the effects of heterosis.

At Myora Farm, the nucleus and multiplier herds share the same environment and management practices; purebred Large White and Landrace sows are raised in exactly the same sheds, with the same feeding regimes and management practices. These similar conditions will allow us to estimate direct piglet heterosis. However F1 gilts will be taken to commercial piggeries in order to perform reproductively, this means that their performance will be recorded under completely different environments and hence maternal heterosis cannot be estimated.

The objective of this chapter is to estimate the direct piglet heterosis for reproductive traits (NBA, TNB, AvBW, Av21dW, NWea and GL). A second objective for this chapter is to estimate inbreeding of the sow and of the litter and to establish for each reproductive trait, the losses produced due to inbreeding depression.

4.2. Literature Review

4.2.1.1. Crossbreeding and Heterosis

The genetic gain resulting from crossbreeding has two origins: complementarity and heterosis (Sellier, 1976). Complementarity is the additive component and heterosis the non-additive component of the genetic basis of crossbreeding effects. The word 'heterosis' was coined by Shull in 1914 (cited by Sheridan, 1981) to describe the increased vigour of crossbred relatives to the average of the parental lines, and thus refers to any favourable departure from additivity in crossbred populations.

The genetic basis of complementarity is primarily the difference in maternal effects between breeds. The practical importance of complementarity is better appreciated when dealing with reproductive traits, e.g. litter size, and in treating them as traits of the generation yielding the final product of the cross. Most of the variation in litter size between crosses is due to "maternal effects" differences between breeding groups used as dam lines (Sellier, 1976). In order to maximize the performance of a population, a crossbreeding program should be designed to capitalize on all forms of heterosis as well as to exploit any maternal effects associated with a particular combination of lines.

Traits closely related to reproductive fitness like litter size and viability with low heritabilities have been described as showing greater inbreeding depression in purebreds and heterosis in crosses; on the other hand, traits less subject to natural selection like individual growth and feed utilization were intermediate in both heritability and heterosis, while carcass traits were highly heritable but not heterotic (Dickerson, 1973).

Sheridan (1981) presented a study done by Winters et al. in 1935, where he compared purebred and first cross populations of pigs using the Poland China, Duroc and Chester White breeds. He compared 76 purebred sows with purebred litters against 46 purebred sows with crossbred litters. The group with purebred litters had an average number of piglets born in total of 9.41 and 8.26 alive; on the other hand the group with crossbred litters had an average number of piglets born in total of 9.79 and 9.19 alive. This represents a direct piglet heterosis of + 4.0% for number of piglets born in total and + 11.3% for number of piglets born alive. Due to the small size of the groups compared, the sampling variation could be partly responsible for such high heterosis. Comparisons like this one made by Winters in 1935 with breeds of pigs with very different origins, present much higher levels of direct heterosis than comparisons between two European breeds as suggested by Rothschild and Bidanel (1998).

A review by Sellier (1976) of 12 studies made between 1961 and 1974 with several breed combinations such as Landrace x Yorkshire, Large White x Landrace, Duroc x Hampshire, Hampshire x Yorkshire among others showed an average direct heterosis effect on litter size at birth of 0.3 of a piglet (+ 3%), slightly lower than the results obtained by Winters et al. (1935) (Table 4-1).

Rothschild and Bidanel (1998) presented a review of several studies where they compared Large White x Landrace crosses against the Large White x Meishan crosses and found a two- or threefold higher heterosis effect for the latter combination. Their review showed that litter heterosis effects lead to slightly larger litter size at birth +0.24 piglets (average of 47 studies), and to higher piglet survival from farrowing till weaning +0.49 piglets or +5.8% (average of 16 studies). Rothschild and Bidanel (1998) concluded that the heterosis values may differ according to breed combinations showing that Large White x Landrace crosses generally exhibit less heterosis than other crosses between European and American breeds' combinations.

The results obtained by Ikeobi (1994) in a study based on Landrace and Large White sows with purebred and crossbred litters in hot and humid environments in Nigeria from 1960 till 1975 showed a 6.4% direct heterosis on litter size at birth. He showed an average of purebred litters of 8.48 piglets born and an average of crossbred litters of 9.02 piglets born, remarkably low for these two breeds commonly used as maternal lines due to their known prolificacy and maternal ability. These high levels of heterosis suggests that the hot and humid environments where the sows were raised as well as the performance levels of the purebred lines are as important as the combination of breeds in the expression of direct heterosis. These results are in line with the concept of genetic homeostasis proposed by Lerner in 1954 (cited by Lynch and Walsh, 1998) in which he established that heterozygotes are expected to be less influenced by environmental effect than homozygotes.

A study by Baas et al. (1992) with purebred and crossbred litters of purebred Landrace and Hampshire sows showed that the averages of both purebred sows with purebred litters were for total number of piglets born (TNB) 10.35, for number of piglets born alive (NBA) 9.71; in addition the average of both purebred sows with crossbred litters from reciprocal crosses was: 11.22 for TNB, 10.68 for NBA. The direct heterosis effect was 0.87 piglets for TNB (+ 8.4%) and for NBA a difference of 0.97 piglets was shown (+ 10%).

In the Netherlands, Katoele (2002) presented a study where two lines and their reciprocal crosses were analyzed. One of the lines was a synthetic line founded from different Piétrain lines; the other one was based on Yorkshire and Large White animals. The raw averages of both purebred lines with purebred litters were 10.76 for TNB and 10.22 for NBA. In addition, the raw average of both purebred lines with crossbred litters from reciprocal crosses was: 11.22 for TNB and 10.68 for NBA. The direct heterosis effect was 0.46 piglets for TNB (+ 4.3%) and 0.46 piglets for NBA (+ 4.5%) although none of these effects were significant.

Katoele (2002) presented raw averages for purebred sows with purebred litters for the trait piglet birth weight (recorded individually) (PBW) of 1.44 kg and for gestation length (GL) 115.2 days; in addition the average of both purebred lines with crossbred litters from reciprocal crosses were: 1.52 kg for PBW and 114.9 GL. The heterosis effect was 60 grams for PBW (4%) and for GL a difference of 0.24 days was shown (-0.02%).

Similar results were obtained by Roehe (1998) in a study done in Germany where an estimate of direct piglet heterosis of 70 grams and 62 grams were shown for a German Landrace and German Edelschwein cross for the trait piglet birth weight (recorded individually) and after adjusting the trait for the litter size respectively. A similar but not significant estimate was presented for a German Landrace and Large White cross. This non significant result is in agreement with a study made by Baas et al. (1992) with Landrace and Hampshire sows where the purebred litters average 1.71 kg for the trait average birth weight (defined as a ratio of litter weight at birth and the total number of piglets born), and the crossbred litters from reciprocal crosses average was 1.70 kg showing no heterosis at all.

Table 4-1 Literature estimates of direct piglet heterosis for reproductive traits.

Source	Breeds analyzed		Midparent average	Direct heterosis
	Number of Piglets Born Alive			
(Sellier, 1976)	12 studies on Western breeds			+ 0.30 piglets
(Rothschild and Bidanel, 1998)	47 studies on Western breeds			+ 0.24 piglets
(Katoele et al., 2002)	Syn (P)	Syn (Y-LW)	10.45	NS
(Sheridan, 1981)	PC - CW - DU		8.73	11.3 %
(Ikeobi, 1994)	LR	LW	8.75	6.40 %
(Baas et al., 1992)	H	LR	10.2	10.0 %
	Piglet Weight at Birth			
(Katoele et al., 2002)	Syn (P)	Syn (Y-LW)	1.48	4.0 %
(Roehe, 1998)	DL	DE		62 gr
(Roehe, 1998)	DL	LW		19 gr (NS)
(Baas et al., 1992)	H	LR	1.70	NS
(Ikeobi, 1994)	LR	LW	1.27	-2.34 %
	Number of Piglets Weaned			
(Sellier, 1976)	12 studies on Western breeds			+0.45 piglets
(Rothschild and Bidanel, 1998)	16 studies in Western breeds			0.49 piglets
(Ikeobi, 1994)	LR	LW	7.75	0.19 %
	Piglet Weight at Weaning			
(Sellier, 1976)	12 studies on Western breeds			+0.5 kg
(Ikeobi, 1994)	LR	LW	4.0	2.81 %
(Baas et al., 1992)	H	LR		3.7 %
	Gestation Length			
(Katoele et al., 2002)	Syn (P)	Syn (Y-LW)	115	-0.02 %

Breeds: PC: Polland China, CW: Chester White, Syn (P): Synthetic breed originated from Pietrain, Syn (Y-LW): Synthetic breed originated from Yorkshire and Large White, H: Hampshire, DL: German Landrace, DE: German Edelschwein, LW: Large White, LR: Landrace.

Rothschild and Bidanel (1998) found in their review that the litter weight at birth showed a direct heterosis effect of 590 grams, and 2.47 kg for the entire litter at 21 days; however the overall means were not presented and a percentage couldn't be obtained. Ikeobi (1994) presented a negative direct heterosis effect of -2.34% in the piglet weight at birth, that became +2.81% when measured at 21 days of age. This occurred because the purebred Large White piglets were born with an average weight of 1.22 kg and had an average daily gain from 0 to 21 days of 90 grams per day. The purebred Landrace pigs were born with an average weight of 1.34 kg and had an average daily gain of 161 grams per day. The crossbred piglets were born with 1.25 kg and had an average daily gain of 132 grams per day.

Sellier (1976) showed in his review for litter size at weaning (at 28 days) a difference of 0.45 piglets equivalent to +6% direct heterosis, and for average piglet weight at 28 days a difference of 500 grams representing a +5% direct heterosis. Baas et al. (1992) showed a 3.7 % direct heterosis for the adjusted weight of the litter at 21 days post farrowing. However no comments were made about the cross-fostering practices in those studies.

4.2.1.2. Inbreeding

Inbreeding is the mating of individuals who are more closely related than the average members of a breed or population (Warwick and Legates, 1979). Related individuals have more genes in common than unrelated individuals, and the closer the relationship, the more genes they have in common (Simm, 1998). Offspring from related individuals tend to become more homozygous and this increase in homozygosity and accompanying decrease in heterozygosity is the underlying reason for the genotypic and phenotypic changes which are associated with inbreeding.

Inbreeding reduces the amount of genetic variation in a population, which is the most important aspect to consider in order to achieve genetic improvement. It can also lead to harmful effects on reproductive rate and general vigor known as inbreeding depression, something well known by breeders and geneticists (Falconer, 1981). Inbreeding depression exists, at least to some degree, for essentially all characters in all populations of diploid organisms (Lynch and Walsh, 1998).

Inbreeding was used by breeders to help fix specific genetic characteristics in an effort to help develop new breeds. During the 1930's in the US several inbred lines of pigs were created for further use in crossbreeding. These lines mirrored the extremely successful results obtained in the hybrid corn business. In pigs these inbred lines suffered from much lower fertility, lower piglet survival rates and some reduction in general performance, so this method was later abandoned (Rothschild and Bidanel, 1998).

A reviewed by Rothschild and Bidanel (1998) on 15 studies showed a decrease of 0.4 piglet born in total for an increase of 10% in the inbreeding coefficient of the sow and a decrease of 0.29 piglets born in total for the inbreeding of the litter. Falconer (1998) presented a study by Bereskin in 1968 that shows a decrease of 0.29 piglets for a 10% level of sow inbreeding with non-inbred litters. These results are in agreement with the results presented by Culbertson et al. (1998) from a study done on a purebred American Yorkshire population showing a decrease of 0.23 piglets per 10% increase in the sow inbreeding. A more recent study made in the Netherlands by Katoele et al. (2002) showed a non significant effect of inbreeding of the sow on NBA, however did find a decrease of 0.24 piglets for a 10% inbreeding of the litter for NBA.

A study by Brandt et al. (2002) based on the Göttingen Minipig, showed a non significant ($P>0.05$) effect on litter size for a 10% increase in the sow inbreeding as well as in the litter inbreeding. This breed of pigs has been selected for reduced size and averages 6.4 piglets born alive with a standard deviation of 2.1 with an average piglet weight at birth of 434 grams with a standard deviation of 103 grams. Despite not presenting an effect on litter size, there was a significant ($P<0.05$) effect on average piglet birth weight caused by a 10% increase in litter inbreeding (+23 grams) as well as sow inbreeding (+60 grams).

Silio et al. (1994) studied the influence of inbreeding on the individual weight of piglets at 21 days of age in lines of Iberian pigs. They concluded that a 10% inbreeding of the sow will reduce the weight at 21 days of the piglets by 1.22 % and 3.63 % for different Iberian lines. A 10% inbreeding of the litter will reduce the weight by 2.2 % and 1.9 % respectively.

Johnson (1990) presented a review where he described the inbreeding depression of the trait gestation length (GL), for a 10% inbreeding level. He found an average decrease in GL of 0.03 of a day with a range starting at -0.20 till +0.22 of a day for the inbreeding of the litter for 3 studies. In addition, he found a -0.28 day decrease in the GL for a 10% increase in the sow inbreeding.

4.3. Materials and Methods

4.3.1. Data description

4.3.1.1. Direct Piglet Heterosis

A combined dataset of Large White and Landrace sows from the nucleus (purebred litters) and multiplier (crossbred litters) herds of Myora Farm was created in order to estimate direct piglet heterosis. Both breeds were combined in a single dataset for comparing the different reciprocal crosses. A description of the number of records of this dataset and the proportion of purebred and crossbred litters is shown in Table 4-2. A total of 18,322 litter records from 4,504 sows were used, with 6,352 (34.7%) purebred litters and 11,970 (65.3%) crossbred litters. The proportion of crossbred litters from 1st parity sows was 97.0 %, this percentage was reduced to 67.2% for 2nd parity sows and further decreased to 61.9% for 3rd parity sows. In parities 2 and 3, Landrace litters (36% and 43.6%) were proportionally more than Large White (30.7% and 34.5%).

Table 4-2 Number (N) and Proportion (%) of purebred and crossbred litters of Large White and Landrace sows

		Large White		***Landrace***		Total	
Parities	**Litter Type**	**N**	**%**	**N**	**%**	**N**	**%**
1st	**Purebred**	75	2.8	55	3.1	130	3.0
	Crossbred	2,582	97.2	1,697	96.9	4,279	97.0
2nd	**Purebred**	698	30.7	525	36.0	1,223	32.8
	Crossbred	1,578	69.3	933	64.0	2,511	67.2
3rd	**Purebred**	644	34.5	541	43.6	1,185	38.1
	Crossbred	1,224	65.5	700	56.4	1,924	61.9
1st to 10th	**Purebred**	3,531	32.0	2,821	38.7	6,352	34.7
	Crossbred	7,500	68.0	4,470	61.3	11,970	65.3

Being the performance at first parity is usually inferior to the performance in later parities; the high proportion of crossbred litters at the first parity can lead to underestimating the difference in performance between purebred and crossbred litters. In order to remove this possible bias a second dataset was created excluding the 1st parity records. There were 13,915 litters in this dataset.

4.3.1.2. Inbreeding

In order to estimate sow inbreeding as well as litter (or piglet) inbreeding, Large White and Landrace datasets were analysed separately. A description of these datasets can be found in Chapter 3. Limits imposed to these dataset were the same as those imposed for the estimation of genetic parameters in Chapter 3 and are presented in Table 3-9.

Three different datasets were compiled for each breed and analysed:

(a) The first analysis was based on a dataset that only contained purebred litters (the nucleus herd), with 3,531 litters from 1,249 sows for the Large White breed analysis and 2,821 litters from 965 sows for the Landrace breed analysis.

(b) A dataset with only crossbred litters (the multiplier herd) was used for the second analysis. There were 7,500 litters from 2,657 sows for the Large White breed and 4,472 litters from 1,752 sows for the Landrace breed.

(c) A third dataset was created by removing the first parity records from (b). There were 4,918 litters from the Large White breed and 2,775 litters from the Landrace breed remaining in this dataset.

4.3.2. Traits Analyzed

The reproductive performance traits analysed in this chapter are described in Table 4-3 for the Large White sows and in Table 4-4 for the Landrace sows with purebred (nucleus herd) and crossbred litters (multiplier herd).

We can observe the high prolificacy of the maternal lines at Myora Farm from Table 4-3 and Table 4-4. The figures presented in these tables are averages over the last ten years (1995 -2004), and compared with the figures presented by APL in their 2003 report (APL, 2003) (average NBA is 10.5 with a range from 8.39 to 11.39), both breeds showed an outstanding prolificacy.

Within Myora Farm's maternal lines the Large White sows showed a higher prolificacy than the Landrace sows. Comparing both nucleus and multipliers herds of both maternal line sows we observed a 1.08 and 0.92 piglet higher litter size (NBA and TNB) on parities 1 to 10 for the purebred litters of the Large White breed compared with the Landrace breed. In addition the difference between crossbred litters is smaller, being 0.29 and 0.34 piglet for both breeds.

Table 4-3 Number of records (N), mean values, standard deviations (SD) and coefficients of variation (CV) in % for Large White sows with pure and crossbred litters for parities 1, 2, 3 and for parities 1 to 10 combined

	Large White sows							
	Purebred litters				**Crossbred litters**			
Parity	**N**	**Mean**	**SD**	**CV**	**N**	**Mean**	**SD**	**CV**
	Number Born Alive (piglets)							
1	75	11.32	2.4	21.2	2,582	10.83	2.7	24.9
2	698	11.62	3.0	25.8	1,578	11.28	3.0	26.6
3	644	12.94	2.9	22.4	1,224	12.00	2.9	24.2
1 to 10	3,531	12.52	3.0	24.0	7,500	11.51	2.9	25.2
	Total Number Born (piglets)							
1	75	12.04	2.6	21.6	2,582	11.57	2.9	25.1
2	698	12.28	3.2	26.2	1,578	11.96	3.2	26.8
3	644	13.93	3.1	22.3	1,224	12.96	3.3	25.5
1 to 10	3,531	13.77	3.3	24.0	7,500	12.46	3.2	25.7
	Number of Piglets Weaned (piglets)							
1	75	8.24	4.3	52.2	2,582	8.04	4.1	51.0
2	698	8.48	3.8	44.8	1,578	8.50	3.9	45.9
3	644	8.09	3.9	48.2	1,224	8.20	4.0	48.8
1 to 10	3,531	7.93	4.0	50.4	7,500	8.07	4.1	50.8
	Average Piglet Birth Weight (kilograms)							
1	24	1.45	0.25	17.2	1,085	1.43	0.24	16.8
2	217	1.55	0.25	16.1	762	1.62	0.27	16.7
3	261	1.52	0.23	15.1	609	1.58	0.25	15.8
1 to 10	1,681	1.48	0.25	16.9	3,649	1.53	0.27	17.7
	Average Piglet 21 day Weight (kilograms)							
1	59	6.03	0.7	11.6	2,072	6.11	0.8	13.1
2	583	6.59	0.8	12.1	1,292	6.57	0.8	12.2
3	526	6.61	0.8	12.1	987	6.64	0.8	12.1
1 to 10	2,821	6.54	0.8	12.2	5,993	6.43	0.8	12.4
	Gestation Length (days)							
1	74	115.48	1.3	1.1	2,580	115.14	1.4	1.2
2	697	115.38	1.5	1.3	1,578	115.29	1.4	1.2
3	644	115.35	1.5	1.3	1,223	115.29	1.4	1.2
1 to 10	3,527	115.35	1.5	1.3	7,494	115.21	1.4	1.2

The Landrace sows presented higher weights at birth and at 21 days, than the Large White sows across all parities and both nucleus and multiplier herds. Comparing parities 1 to 10 for both nucleus herds we observe a 90 gr and 290 gr weight advantage for the Landrace breed in the AvBW and Av21dW, respectively. These differences decrease to 50 gr and 160 gr when both multiplier herds are compared.

Gestation length for Large White was 0.48 and 0.47 day shorter than for Landrace sows at the nucleus and multiplier herds. In addition, comparing the nucleus versus the multiplier herds of both breeds, a decrease in gestation length of 0.15 and 0.14 days respectively was observed.

The trait NWea was defined as the number of piglets weaned from each sow that farrowed at least 2 piglets born alive. Litters from those sows that were used as foster sows and raised a second litter in the same farrowing period, were excluded, and hence only the first litter was considered. This is the reason why the trait NWea weaned has a raw average around 8 and not around 10 as it would have if the second litter was also considered.

Nevertheless there is no significant difference between both nucleus herds for the trait NWea. There is no significant difference between the nucleus and multiplier herds of the Landrace breed for this trait either. In contrast, Large White sows at the nucleus herd weaned 0.18 piglets more than sows in the multiplier herd. This trait is highly influenced by management practices such as cross-fostering of the litters trying to even the numbers weaned by each sow.

When analyzing litter inbreeding as well as direct piglet heterosis the assumption that all piglets in the litter had the same levels of inbreeding and heterosis was made. Due to cross-fostering made at Myora Farm, the piglets will be moved between sows to maximize the performance of all sows farrowing in the same batch. Purebred Large White, Landrace and even Duroc piglets as well as crossbred (LW x LR) and (LR x LW) piglets if removed from their biological mother will be allocated to the best possible sow at that stage regardless of her breed (LW, LR or Duroc). This management practice is not recorded, so in the case of traits recorded at 21 days post-farrowing (NWea and Av21dW) the piglets will be allocated to the inbreeding coefficient and the direct piglet heterosis of the litter they are raised in, regardless if they were fostered piglets or not.

Table 4-4 Number of records (N), Mean values, Standard deviations (SD) and coefficients of variation (CV) in % for Landrace sows with pure and crossbred litters for parities 1, 2, 3 and for parities 1 to 10 combined

	Landrace sows							
	Purebred litters				Crossbred litters			
Parity	**N**	**Mean**	**SD**	**CV**	**N**	**Mean**	**SD**	**CV**
	Number Born Alive (piglets)							
1	55	10.91	2.6	23.8	1,695	10.54	2.6	24.7
2	525	10.77	2.8	26.0	933	11.08	2.7	24.4
3	541	11.89	2.7	22.7	700	11.86	2.7	22.8
1 to 10	2,821	11.44	2.8	24.5	4,470	11.20	2.7	24.1
	Total Number Born (piglets)							
1	55	11.76	2.7	23.0	1,695	11.19	2.7	24.1
2	525	11.49	3.0	26.1	933	11.74	2.8	23.9
3	541	12.99	3.0	23.1	700	12.91	2.8	21.7
1 to 10	2,821	12.85	3.1	24.1	4,470	12.12	3.0	24.8
	Number of Piglets Weaned (piglets)							
1	55	7.33	4.5	61.4	1,695	8.01	4.24	52.9
2	525	8.26	3.9	47.2	933	8.84	3.8	43.0
3	541	8.45	3.8	45.0	700	8.66	3.86	44.6
1 to 10	2,821	8.05	4.0	49.7	4,470	8.23	4.1	49.8
	Average Piglet Birth Weight (kilograms)							
1	24	1.45	0.15	10.3	889	1.52	0.23	15.1
2	188	1.66	0.30	18.1	623	1.67	0.26	15.6
3	244	1.62	0.25	15.4	462	1.62	0.25	15.4
1 to 10	1,447	1.57	0.27	17.2	2,707	1.58	0.25	15.8
	Average Piglet 21 day Weight (kilograms)							
1	41	6.22	1.05	16.9	1,335	6.25	0.79	12.6
2	423	6.84	0.8	11.7	782	6.71	0.74	11.0
3	444	6.90	0.7	10.2	579	6.86	0.72	10.5
1 to 10	2,248	6.83	0.8	11.7	3,575	6.59	0.79	12.0
	Gestation Length (days)							
1	55	115.84	1.48	1.28	1,694	115.50	1.41	1.22
2	523	115.88	1.44	1.24	932	115.85	1.44	1.24
3	541	115.69	1.43	1.24	699	115.81	1.39	1.20
1 to 10	2,817	115.83	1.44	1.24	4,464	115.68	1.41	1.22

4.3.3. Statistical Analyses

The analyses of direct heterosis effects as well as inbreeding were done implementing a mixed model with a restricted maximum likelihood methodology using the ASREML software (Gilmour et al., 2002). A separate univariate animal model was used for estimating direct piglet heterosis for each reproductive trait as well as for estimating the effect of sow and litter inbreeding on each reproductive trait. A repeatability model was implemented for the entire dataset as well as the nucleus and multiplier datasets where more than one record corresponded to one sow.

The mixed model equations used in the uni-variate analyses with repeated measurements can be written in matrix notation as:

$$y = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e} \qquad [4\text{-}1]$$

Where **y** represents a vector of observations of different reproductive traits, **b** represents a vector of fixed effects, **u** represents a vector of additive genetic effects ~ $(\mathbf{0}, \mathbf{A}\sigma^2\mathbf{a})$, **p** represents a vector of permanent environmental effects and **e** represents a vector of residual effects ~ $(\mathbf{0}, \mathbf{I}\sigma^2\mathbf{e})$. The matrix **X** is the incidence matrix relating observations with fixed effects; the **Z** matrix is the incidence matrix relating observations to animals and the **W** matrix is the matrix relating observations with permanent environmental effects; **A** is the additive genetic relationship matrix and **I** is the identity matrix.

Fixed Effects:

Fixed effects included in **b** were described in Table 3-12 of Chapter 3. In order to obtain an accurate adjusted overall mean, the factors were constrained in ASREML to avoid the setting of one level of each factor to zero and deriving all the other levels from this one.

Random Effects:

Random effects used in these analyses were the additive direct genetic effect of the sow as described in Chapter 3 and the permanent environmental effect of repeated records of the sow.