

Genetic Selection and Advances in Swine Breeding: A Review of its Impact on Sow's Reproductive Traits

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ABSTRACT

Until now, continuous selection and breeding of swine is done to take advantage of increase reproductive efficiency. Litter size at birth and weaning are important traits of interest by pig breeders as it affects farm productivity. However, factors such as uterine capacity, fetal survival, stillborn, individual birth weight, and post-natal interaction of piglets and sow limits improvement of this trait. Although continues conventional breeding and selection facilitates progress in lowly heritable reproductive traits, success has a consequence of non-uniform piglet with lower birth weight which led to increase pre - weaning mortality. Pig breeders therefore shift selection strategy from large litter size at birth to increase in litter size at weaning. On the other hand, rapid improvement in reproductive trait observed in the past decades is due to extensive effort of record keeping, conventional and genomic selection, Genome Wide Association Study/Analysis that determine potential candidate gene and use of Best Linear Unbiased Prediction (BLUP) that account the genetic merit of certain breed across generation. Innovations brought by this reproductive strategy further optimize breeding scheme efficiency which speed up genetic progress, allowing only breeds with superior reproductive traits to reproduce for the next generation. Today, it is possible to produce more than 30 piglets weaned/sow/year due to improved genetics. Further development would be expected in the future for litter size and piglets born alive with the utilization of ESR gene, crossing of Meishan to white breeds and with application of genomic selection, GWAS and BLUP.

Keywords: Reproductive traits, genetic selection, breeding, sow

INTRODUCTION

Performance of swine is dependent on genetics, environment, and its interaction. Typically, sow reproductive traits among dam lines is improve by way of crossbreeding and selection. However, most sows' reproductive traits have low heritability wherein pig breeders have difficulty in achieving positive and significant improvement. Likewise, differences in reproductive traits could be attributed to environmental variability. The interaction of multiple genes/genotype control both productive and reproductive traits (Cassady and Robison, 2006) and this set the upper limit for the performance of swine in a certain environment. Therefore, capitalizing in breed development is vital as some genetic modifications in reproductive traits will be embedded and carried out by the animal for a lifetime. The increasing population and demand for pork in the market pressured pig breeders to develop and exploit the potential productivity of sows in terms of producing large litter size at birth and weaning and increase number of piglets weaned per sow per year. However, these traits of economic importance which contribute profitability to the farm are hard to improve and have negative genetic correlation with number of stillborn and pre-weaning mortality. Thus, to impact swine reproductive efficiency, this factor must be overcome in any possible way.

Monetary value placed on reproductive traits improvement serve as primary factor for genetic selection. Over the past decades, relative progress in selection and breeding were attained. It was highlighted in the review of Tokach et al., (2016) that advances in genetics for the last 30 years had been facilitated by the implementation of technology relative to reproductive efficiency from manual record keeping to detailed computerized production, visual or single trait selection to BLUP with marker assisted selection and pen mating to artificial insemination with highest indexing boars. This milestone in pig breeding has reached the era that maximize utilization of genomic -assisted selection to improve lowly heritable traits and reproductive efficiency. With this rising advancement in science and technology, the present review will assess how far continuous effort of selection and breeding using conventional and sophisticated technology improve economically important reproductive traits and to what extent it contributed to the development of swine industry.

Litter Size at Birth and its Correlation with Ovulation rate and ESR gene

Litter size at birth is considered as trait with lower heritability (Bidanel, 2011) which is approximately 0.10 and normally controlled by ovulation rate, uterine capacity, embryonic/fetal survival. The complex interaction of this factors suggest that litter size is a hard to improved trait which needs ample of time for selection and breeding to realize development. Manipulation of either ovulation rate or uterine capacity did not promote considerable impact on litter size (Bennett and Leymaster, 1989), instead index selection for both ovulation rate and embryo survival could be a possible strategy to achieve development (Johnson et al. 1984). By contrast, Rutherford et al., (2013) noted that direct selection for post-natal piglet survival is the most effective strategy to increase the litter size. Traits such as litter size and average birth weight were

genetically and negatively correlated and acted antagonistically on mother and off spring (Matheson et al., 2018). Hence, application of selection for litter size causes variation in birthweight (Kemp et. al., 2018) which affect the number of pigs born alive (PBA) in each parity. In addition, selection for this trait increases piglet mortality due to negative genetic correlation (-.23) of piglets born alive and stillborn (Restelli and Pagnacco, 2003). It should be noted that later parities increase the possibility of producing stillbirth which was commonly observed in small litters (Canario, 2006). Conversely, selection performed by Bolet et al., (2011) for 17 generations within sire family resulted an increase of 1.4 piglets per litter. Generally, teat number is one of the bases in selecting sows that determine litter size. This trait has 0.4 (Knol et al., 2016) or 0.365 heritability estimates (Tan et al., 2017) that can be recorded for both sexes during selection without measurement error and therefore considered as a trait where genetic analysis reach a highest accuracy. As reviewed by Kemp et. al., (2018) selection for litter size affect reproductive physiology and welfare of sow as well as the well-being of the piglets.

Production of large litter size is made possible by increase in ovulation rate. Normally, sows are capable of ovulating 15 to 20 ova every estrus period with 90% fertilization rate. Owing to limited carrying capacity of uterus, only 60 -70% out of the 90% fertilize egg cell were successfully developed and formed as alive piglets at birth (Pope and First, 1985).It turns out that uterine capacity is a limiting factor for the development of oocytes and that physical, biochemical and morphological limitation of uterus include space, nutrients, gas exchange and surface of the placenta (Wahner and Brussow, 2009). Although selection for ovulation rate can increase the number of ovulating follicles, this higher heritability (0.39) of ovulation rate at puberty and fertilization cannot be correlated to litter size (Rosendo et al., 2007), and selection for this trait is often

associated with risk of higher mortality due to large litters. The increase of ovulation rate also reduced probability of pre-natal survival (Haley and Lee, 1993). On the other hand, Johnson et al., (1999) conducted selection for litter size based on index using corpora lutea and fetuses at 50 d and their result showed an increase of 0.9 piglets born alive per litter. In addition to this, after 11 generation of index selection for ovulation rate, an increase of 7.4 and 3.8 in the number of ova and fetuses were achieved, respectively. This result is in agreement with the findings of Zimmerman and Cunningham (1975) in their five generation selection experiment for ovulation rate in which they were able to increase average ovulation rate from 14.38 to 16.19 with an average of 1.18 selection differential per generation. Likewise, Lamberson et al., (2011) reported that response to selection for ovulation rate in nine generations for a 14 breed composite population resulted in litter size increase of 1.8 pigs and 1.4 pigs per litter when regression method and animal model were used respectively.

With the advent of genetic technology, more focus is given to specific genes that control the litter size of pig. The identification of ESR (estrogen receptor) gene as a major gene affecting litter size pave the way in exploring the possibility of producing more piglets at birth. This received a lot of attention over the last decades since it can be used as a genetic marker for litter size in the landrace breeding scheme (Wu et al., 2006). This commercially available gene marker was first discovered in the Chinese Meishan breed and later in large white and Landrace population. Between the two popular dam lines, it appears that ESR genes is more likely to be present in large white population than landrace with an effect of .8 to 1 pig per litter. Furthermore, the effect of this gene on litter size was confirmed by Rothschild et al., (1996) in which synthetic lines with 50% meishan genetic background that were homozygous for allele B in estrogen receptor (ER) gene produced 2.3

more pigs in first parities and 1.5 more pigs averaged over all parities than females from the same synthetic lines and homozygous for the undesirable allele. The increased in litter size of more than 20% found in their study implied that ESR gene could predict differences in litter size across population. Another, Rothschild and Plastow (1999) achieved 30% increase in litter size integrating ESR genotype in dam lines selection index. Although this result is quite promising, meishan's slow growth and excessive fat characteristic is a great challenge to swine breeders in developing a breed with more litter size and leaner meat. In spite of that, it is undeniable that ESR gene could be used as genetic markers to track the genetic merit for increase of litter size across generation especially for prolific swine breeds such as Large white, Landrace, Meishan and their crosses.

Stillborn, Piglet Survival and Number of Piglets Weaned

Piglets found dead behind the sow after parturition is categorized as stillbirth in commercial herd setting (Dial et al., 1992). It is estimated that 10% of piglets are stillborn during parturition (Langendijk and Plush, 2019). This possibility of stillbirth is 1.4 times greater in piglets from litters with assistance during farrowing than in litters without assistance (Canario et al., 2006). In a large-scale swine production, an estimated 11.5% out of 23.1% piglet mortality is caused by stillborn. It only indicates that stillborn was 3 to 6 times greater in terms of caused in piglet mortality than other mortality traits. Furthermore, this trait has 0.08 heritability on the sire whereas 0.24 for the dam component which suggest that selection on parent sow can reduced piglet mortality (Strange et al., 2013). Weight at birth is another factor that increased stillborn incidence in pigs and is known to be negatively correlated with decreased in birth weight and increased in litter size (Johnson et al., 1999). It is also significant to note that male piglets have 2-4% lower probability of survival than their female

counterpart (Knol et al. 2002a). Segura-Correa and Solorio-Rivera (2013) determine risk factors of stillbirth and mummified fetuses and suggest that as litter size increases the risk associated with stillbirth and mummified fetus also increases.

Piglet survival depends mainly in three factors such as piglet quality, sow characteristics and the interaction between sow and piglets. Proper evaluation of this traits and selection based on individual birth weight, litter size and weaning to estrus interval is an ideal technique to increase number of weaned piglets per sow per year (Roehe and Kalm, 2000). However, negative genetic correlation of litter size with pre-weaning survival exist in pig breeds (Rothschild and Bidanel, 1998). In contrast, rate of pre – weaning mortality is related with piglet individual birth weight which increased exponentially when individual birthweight decreased from 2.1 to 0.5kg (Roehe and Kalm, 2000). Birth weight has higher heritability estimate (0.29) which can be easily improved thru selection. Though it was the case, heavier piglets may likewise encounter difficulty of going out in vaginal canal resulting to longer parturition duration and increase risk of being blocked which could lead to hypoxia/decrease oxygenation and eventually death (Fahmy et al., 1978; Langendijk and Plush, 2019). Therefore, a balance selection between birth weight and liter size is necessary for piglet survival. As piglet birth weight and number of piglets born alive in litter are negatively correlated, piglet uniformity rather than increase in litter size is now considered during selection.

Number of piglets weaned is a function of litter size born alive, pre-weaning mortality (Koketsu et al., 2017) and fostered piglets. Heritability of this traits is relatively low (0.06) and swine breeders struggle and had a slight success in selection for this trait due to cross fostering effect (a non-genetic influence). Increase in piglets weaned require a greater number of functional teats and this set as limiting

factor for the number of weaned piglets per sow (Knol et al., 2016). It was stated by Popovac et al., (2012) that heritability coefficient for the number of live born, total number of born, stillborn and reared piglets in the litter are low ($h^2=0.056$ to 0.142). This observed lower heritability value for the number of reared (0.056) and total number of born piglets in the litter (0.142) are connected to reproductive traits which indicate the important influence of the surrounding environment in the fertility of pigs. Conversely, Rutherford et al., (2013) reported in their review that Denmark national litter size weaned between 1996 and 2011 increased from 9.9 to 12.7 with 2.8 difference in contrast to only 0.6 piglets increased in live born litter size for UK in the same span of years. This difference could be attributed to better reproductive efficiency, nutrition, management, and environment.

Number (Piglets) Born Alive and Uterine Capacity

Piglets born alive in first parity increases with increase age of gilts at first mating (Iida et al., 2015). However, piglet mortality remains a big challenge and account for about 20-25% in modern pig production (Alonso-Spilsbury et al., 2007) wherein 50% of this occur in the first 2-3 days after birth (English and Morrison, 1984). As such, during selection, it is ideal to consider traits such as number of healthy piglets born to increase number of births and decreased mortality rate (Ye et. al., 2018). Nielsen et al., (2013) suggest to practice selection for litter size at d 5 after farrowing (LS5) to improve total number of piglets born and reduce mortality rate. On the other hand, after 14 generation, Johnson et al., (1999) stated that response to selection for increase ovulation rate and embryo survival were additional 3.0 and 1.4 pigs total number of born and number of born alive, respectively. On the contrary, selection for number of pigs born in total (NOBT) and the number of pigs born alive (NOBA) may increase the risk for stillborn

or pigs born dead (Roehe and Kennedy,1995). Despite of this, higher genetic correlation, and similar heritability between number of pigs born in total and number of pigs born alive implied that selection for this trait often result to similar response (Roehe and Kennedy. 1995). Furthermore, number of pigs born alive has lower heritability with phenotypic variance of (0.001-0.40) detected by genome markers under farm management and environmental influences (Onteru et al., 2011). Though, it is difficult to improve this traits, the high genetic correlation coefficient ($r=0,947$, total correlation) of total number of born and number of live - born piglets found by Popovac et al., (2012) indicates that selection for increase number of piglets born alive per litter can be achieved. However, even if increase of piglet born alive is attainable, the 15 – 20% of those are at an increased risk of suffering from asphyxia at birth which will likely result to death and morbidity (Langendijk and Plush, 2019).

Uterine capacity is defined as the ability of the uterus to support the development of fertilized egg cell until farrowing. The potential for increase in piglets born alive is possible through changes in uterine capacity, placental and fetal functions, since uterine crowding and sibling competition (space and nutrition) are factors that influence piglet welfare and vitality (Kemp et al., 2018). According to (Hruska, 2000), uterine length and capacity may be improved by genetic selection for this trait, genetic selection or hormonal manipulations that will result in reduced placental size and/ or increased placental

efficiency, marker assisted selection or other treatment schemes to improve fetal erythropoiesis during early and late gestation. Regardless of fetal genotype, uterine environment determine placental size (i.e., surface area, length, and weight) up to 90 days of gestation (Biensen et al., 1989), hence selection for increase number of piglets born alive may result in piglets suffering from intrauterine growth retardation and consequently in smaller litter size. In light of this, Matheson et al., (2018) suggests that the proportion of intrauterine growth retardation IUGR-affected piglets in a litter is a suitable indirect measure of uterine capacity for inclusion in breeding programs that aim at reducing IUGR in piglets and improving piglet survival. The abovementioned circumstance place animal breeders in a dilemma in choosing between number of piglets born alive and piglet viability at birth. Depending on their strategy, swine breeders may choose to select for either increase litter size or piglet uniformity or viability. In different circumstance, backcrossing of large white hyper prolific sows strain to sons of similar prolificacy for 20 years resulted in increase of 2.6 pigs per litter and 1.5 pigs per litter born alive or a genetic superiority of 1.4 pig/liter born alive (Bidanel et.al, 1994). With the rising knowledge in genomic selection, Web (1998) speculate that extra 4 piglets born alive per litter in the next 10 years is attainable thru the combination of Best Linear Unbiased Prediction (BLUP), Meishan genes and ESR.

Table 1: Heritability estimate (h^2) for female reproductive traits Summarized by Rothschild (1996).

Female Traits	h^2	
	Mean	Range
Age at Puberty	0.32	0 – 0.64
Ovulation rate	0.39	0.10-0.59
Embryo survival	0.30	0.05 -0.40
Litter size born	0.10	0-0.76
Litter birthweight	0.29	0.054
Number born alive	0.07	0.066
Number weaned	0.06	0-1.0
Piglet survival to weaning	0.05	0-0.97
Weaning to estrus interval	0.23	0.03 – 0.36
Farrowing interval	0.20	0.14 – 0.36

Variation in reproductive traits within commercial dam lines and Meishan breed

Large white and Landrace are known for their excellent maternal performance in commercial setting. For large white breed, 2nd and 3rd parities are which optimum reproductive performance is generally attained (Ye et al., 2018). First and second parity genetic correlation for Yorkshire and Landrace breeds were .59 vs .90 (number of pigs born in total) .49 vs .93 (number of pigs born alive) and .17 vs .81 for number of weaned pigs respectively (Roehle and Kennedy 1995). The high genetic correlation for traits in Landrace suggests that they are more likely to perform well in certain environment. Although selection for the same traits occurs in this dam lines, there are still differences in reproductive performance. For instance, the average total number of born for large white is 14.2 while 14.6 for the Landrace (Bidanel, 2011). On the other hand, longevity performance traits of pure breed and crossbred sow have no significant or zero genetic correlations. Sow remaining in the nucleus herd for at least 2 parities is not indicative of her offspring's longevity at the commercial level (Abell et al., 2016). Kraeling and Webel, (2015) claimed that early parity performance determine crossbred sow's lifetime performance in a commercial herd, though genetics, nutrition, housing, disease, lameness, age at first mating, assistance at farrowing, length of lactation and growth rate, body condition and performance of parity one impact sow longevity. Stillbirth is an important factor that affect sow's productivity in commercial herd. Highest case of stillbirth and decrease in birthweight was observed in large white sows and lowest in Meishan sows when litter characteristics were compared in 4 genetic types of sows including F1 Duroc × Large White sows, Large White sows, Meishan sows, and Laconie sows (Canario et al., 2006). Reproductive performance in purebred Landrace and Yorkshire sows showed no differences in number of stillborn per litter and weaning to

conception interval but Landrace sows had significantly higher number of total born per litter, number of live born piglets per litter and average piglet birthweight compared with Yorkshire sows (Tantasuparuk et al., 2000). In addition, lower heritability values for number of weaned pigs compared to number of pigs born in total (NOBT) and the number of pigs born alive (NOBA) was observed in Landrace and Yorkshire breed (Roehle and Kennedy, 1995). This conforms to the findings of Ye et al., (2018) who reported that heritability estimates lower than 0.10 was found in eight reproductive traits in large white population and two of which includes total number of born (TNB) and number of born alive (NBA).

Meishan breed gained popularity in swine breeding for its outstanding performance of being prolific. This swine native in some part of China reach puberty 100 days earlier and exhibit shorter weaning to estrus interval compared to western swine breeds (Bidanel, 2011). Higher uterine capacity of Meishan sows compared to Large White sows enables it to carry a greater number of embryos throughout gestation period (Haley and Lee, 1993). Meishan conceptuses have a greater fetal weight: placental weight ratio than Yorkshire conceptus across both uterine environments (Biensen, 1998). Meishan is also excellent in litter size and piglet survival (Haley and Lee, 1993). Despite higher litter size and lower birthweight, survival rate of litters from Meishan breeds is the same as the large white litters (Haley and Lee, 1995). In one study, 25% Meishan genetics crossed to white breeds allow increased in litter size but in expense with low growth rate and poor-quality lean carcass content (Hall et al., 2002). This emphasize that hybrid vigor for large white and Meishan are much higher than normal crosses between large white and Landrace. Nevertheless, a difference of only one piglet for total number of born in favor of Meishan breed compared to large white was found in the study of Canario et al., (2006).

Genomic Selection and Its Merit on Sow's Reproductive Traits

Phenotypic selection is a tedious activity that requires a lot of time for intensive measurement of lowly heritable traits. Over recent years, advances in genomics and development of panels, quantitative trait loci, and marker assisted selection paved the way in addressing this problem. Application of genomics selection proposed by Meuwissen et al. (2001) nowadays facilitates the rapid genetic progress in swine industry. In particular, the Gene - Assisted Selection (GAS) were used effectively in pig breeding scheme to increase the genetic gain and economic returns (Li et al., 2007). Genetic gain on this aspect was achieved by tracing the level of inheritance through genome-wide genetic marker data or marker genotype distributed in the entire genome to estimate the genetic merit of individual candidate animals. Consequently, better response and accuracy of selection for a trait with genetic markers (Meuwissen et al., 2001) improved pig breeding scheme efficiency in terms of reliability, genetic trends, and inbreeding rate without any need to modify their current structure (Tribout, et al., 2012). In addition to, a performance record which was analyzed for Landrace herd in China shows a possibility of increasing 25% in genetic gains for traits with low heritability applying the genomic selection technology (Zhang et al., 2016). Though this finding is interesting, Samore and Fontanesi (2016), concluded in their review that caution must still be taken into account when using genomic selection in its implementation considering limits and problems as this represents the strategy of choice in pig breeding.

In conventional breeding, reproductive traits can only be measured after farrowing of sows, however, genomic markers able to detect these traits at early age and thus decreased generation interval. Regardless of prevailing environment, genetic make-up of individual will not change. Hence, identification of superior

breeds that carry outstanding genes responsible for reproductive traits is significant during selection. Marker Assisted Selection (MAS) utilizes genetic markers information to easily assess breeder's trait of interest. Unlike conventional selection and breeding programs, MAS allows precise selection without progeny testing. Though, MAS further improves accuracy of estimated genetic breeding value (EGBV), its application is only ideal to monogenic traits and restricted in reproductive traits with low heritability. Furthermore, the advantage of using this technology must offset the additional cost required for DNA isolation, genotyping, and phenotypic data collection. In the review of Wakchaure et al., (2015), they mentioned that MAS is beneficial in combination with traditional selection techniques when the traits are difficult and expensive to measure with low heritability such as recessive and reproductive traits. However, application of marker-assisted selection also requires continued effort for recording phenotypic traits to enhance quantitative trait loci detection, facilitate accurate estimation and confirmation of effects and proper use of these estimates in selection (Dekkers, 2004). Since genetic analysis in swine population assists in identifying traits that can be passed by parents to offspring, Bjerre et al., (2010) recommend using several markers to facilitate efficiency of marker-assisted selection.

The advent of genome-wide association studies/analysis (GWAS) and discovery of 60K SNP panel for pigs in 2009 promote accurate genetic evaluation and selection in candidate breeding animals. This breakthrough starts the application of genomic selection for genotyping large quantity of data. Genome-wide association (GWA) serves as a valuable tool for examining functions of genomics and provides effective means in determining genetic variation and candidate genes of farm animals. A study by Wang et al., (2017) using GWAS in a large white pig population provides knowledge on

genomic variation and candidate genes that are involved in the genetic mechanisms of piglet uniformity (PU) and Farrowing Interval (FI). Likewise, Zhang et al., (2019) discover eleven (11) candidate genes TXN2, KCNA1, ENSSSCG00000003546, ZDHHC 18, MAP2K6, BICC1, FAM135B, EPHB2, SEMA4D, ST3GAL1, KCTD3, FAM110A, TMEM132D, TBX3, and FAM110A associated in reproductive traits of duroc pig population. Moreover, Tao et al. (2013) identified TCF12, CTNNAL1, and WNT10B as candidate genes for litter size. Identification of candidate gene through polymorphism led to GWAS which validate that gene is associated with the traits of interest in the population. Notably, candidate gene approach is widely use technique for comprehensive analysis of genetic variability within population.

The introduction of Best Linear Unbiased Prediction (BLUP) technology further enhances genetic gains and maximized the reproductive performance of superior breed. It employs accurate estimation of breeding value by measuring

the traits and their relatives to assess genetic potential and rank individual animal based on its genetic merit. This allows swine breeders to have faster genetic gains compared to conventional breeding and enable them to make accurate decisions considering the economically important traits. Additionally, with the help of BLUP, accurate prediction of genetic merit of all pigs across different generation can be achieved by separating environmental effects from genetic influences (Web, 1998). This promising technological advancement in breeding and selection help swine breeders in designing thorough breeding scheme that eliminates poor performing animals in the population by putting strong emphasis on records of relatives with superior genetic make-up. Indeed, the use of BLUP substantially improves the response of selection compared to sib-index (linear combination of phenotype, full-sib average, and half-sib average) or phenotypic deviation (Keele et al.1998).

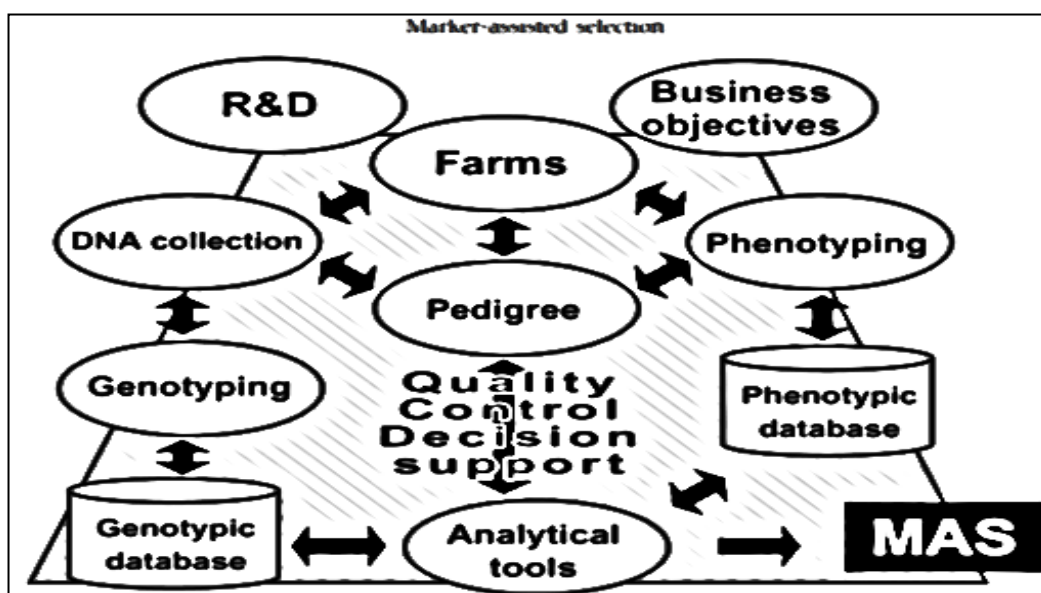


Figure 1: Components of an integrated system for the use of molecular genetic information in breeding programs for Marker-Assisted Selection (MAS) (Dekkers, 2004)

CONCLUSION

Improvement in reproductive traits means profit in swine industry. To cope up with the growing demand for pork in the market, pig breeders must invest effort

particularly in increasing litter size at birth and weaning. However, several factors such as uterine capacity, fetal survival, and teat number may limit productivity of sow in producing large and uniform litter size at

weaning. Moreover, as piglet born alive increases, incidence of stillborn and piglet mortality rises concurrently. The challenge therefore lies with the holistic application and utilization of dam lines with ESR genes, crossing of meishan breed with either Landrace or Yorkshire and using genomic selection, GWAS and BLUP. Also, incorporating conventional selection program with new selection strategy such as genomic selection to maximize sow genetic potential is vital for the realization of development. Although, environment, management and nutrition are factors which contribute to its progress, this aspect can easily be addressed and implemented within the farm. Today, highly prolific dam lines can achieve 25 to 30 ovulation rate per estrus. In the future, 30-40 piglets weaned/sow/year will be possible with excellent genetics and sow management (Koketsu et al., 2017) but this might be with the expense of lower birth weight, increase rate of stillborn and poor post weaning piglet quality. Hence, continuous undertaking to exploit and reach the peak of sow's genetic potential must be done to address this challenge and constraint. While genetic progress leads to increased economic returns, it is important to find the proper balance between progress and economics, as the system that leads to the highest genetic gain may not be the most profitable considering the willingness of customer to pay extra amount for improved genetic quality.

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