Latest news on gilt and sow reproduction II: Impacts of pattern of prenatal loss in sows on postnatal growth performance

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1. Introduction

We recently reviewed research and development priorities that would be of immediate benefit to the growth and sustainability of our food animal industry. From this review we determined that the future competitiveness of our meat industry would depend on the technological information that allowed producers to "place the right genetics in the right environment to produce the right product". By the "right product", we accept that product criteria that might presently allow producers to compete for the sale of generic meat (pork) products in the global market place may need to be replaced by competition in markets that have very different requirements. The product "differentiation" presently mainly relates to specific market requirements in terms of the appearance and nutritional quality of the product that will acceptable. However, there are also increasing requirements in terms of the production environment in which the food animals are reared and animal products are processed. Obvious requirements might include nutrition, age and maturity at slaughter, and processing techniques used, to insure the appearance and acceptability of products at the retail level.

Political motivation to create barriers to global pork marketing cause additional problems for market accessibility, which are often beyond the control of even corporate pork producers. Interestingly, some of the more extreme requirements for gaining market access seem in the case of the UK to have failed to achieve their primary objective. Although producers may be in full compliance with all aspects of production guidelines and Quality Assurance (QA) requirements affecting pork production within that country's jurisdiction (say the UK), their costs of production do not allow locally produced pork products to compete with products of out-of-country producers who gain market access without having to meet equally stringent production requirements in their home country. Thus one the one hand, considerable political attention is paid to the demands of a relative small, but highly motivated, group of consumers, resulting in legislation that considerably increases production costs for producers locally. The misguided perception seems to be that such legislation represents the "enlightened and responsible view" of the majority of consumers. However, when one analyzes consumer purchasing choices, even if product labeling clearly identifies the production systems from which the products originated, most consumers purchase their bulk food supplies on the basis of price. Therefore, as products like pork become increasingly traded on a global basis, there may be considerable risks to applying anything other than globally accepted requirements on pork production, if governments want their producers to be in a competitive situation. It seems that this is particularly important when the general demands to meet high standards of welfare, food safety and environmental sustainability are often highest in those countries that eventually become less competitive in the global market place. Why take such high quality production out of the growing world pork market, simply to have these retail needs met from production in country's with lower welfare and environmental standards. Perhaps the greatest progress to improving the overall standards of food-animal-production world-wide, will he achieved by making the producers with the highest standard, more, rather than less, competitive in the marketplace?

What relevance do these opening comments have to the topic of this lecture? Firstly, a personal belief that by providing opportunity to our best producers to be competitive, we can help them to achieve levels of production efficiency and sustainability which will allow them to survive. In part this interaction relies on a more intimate link between identifying a market opportunity and refining the technology and entrepreneurial skills to capture this opportunity. Secondly, the possibility that although the increasing scale of integrated production systems offrers great advantages in terms of input costs, these gains seem to be offset by reduced efficiency at the primary production level, seems to offer opportunities for more efficient, yet smaller production systems, to remain competitive. By adopting the "Henry Ford" philosophy, big systems are expected improve overall efficiency and net profitability by mass production of a standard product. In terms of products derived from purely physical materials, this is probably very achievable (every Model-T can be exactly the same and is always black). However, in a business like pork production, the very basis of "product" development through genetic selection is dependent on the existence of biological variation. Taking advantage of this variation in genetic improvement programs is the way to the future. Failing to recognize and either reduce, or account for, this variation at production level, results in massive inefficiencies in our industry.

Large-scale pork production may allow variation at the animal level to be ignored to a point, in that other parts of the value-added food chain may allow the economic burden of the production-level inefficiencies to be acceptable. However, increasing knowledge of the causes of this variation, and acceptable strategies at production level to either reduce or account for this variation with improved production technologies, offers other alternatives. Are the welfare and environmental costs of keeping 20 or 30 percent more sows in production than is needed to meet the production goals set for marketable product going to be acceptable in the longer-term? If other producers choose not to capture these efficiencies in production efficiency, does this allow an opportunity to remain competitive by achieving these greater efficiencies in your own system?

This also seems to be a question about the philosophical approach that will guide the future of pork production. The drive to lower unit input costs per kilo of pork product seems to increasingly demand larger production systems. However, contrary to the Henry Ford philosophy, this seems to result in poorer control of production processes and increased inefficiency at the animal level. In turn this leads to problems with employee motivation and retention. At the animal level, the price paid is a growing concern. A system that might be justified as serving the minimal requirements of the "average" pig, leads to poor production and retention of the pigs to either side of this average, and the morale and environmental acceptability of this situation needs consideration. Perhaps the best comparisons of acceptable, and truly competitive pork production for the global marketplace in the future, should place a clear (monetary) value on all components of pork production. What is the true cost of producing pork if it is expressed on the basis of input costs per kilo, less the environmental and social price paid for each kilo of pork produced. Legislation to promote sustainable production can work, but as discussed above may produce very variable responses if imposed at a national level. In the era of Kyoto and international agreements on global trade regulations, some comparisons of production efficiencies that include estimates ratios of nutrient loss per kilo of pork produced would start to allow a fairer comparison by major importers of pork products of the real costs of production. In this situation, even if producers were required to adopt different production practices, or chose alternative production systems voluntarily, the net cost of producing the product would be clear to the consumer. On the one hand, this might alert us to the increasing cost of taking the least-cost approach to pork production. It might equally indicate that the true cost of producing organic and other products for niche markets is not likely acceptable in terms of meeting the future consumer demands for pork on a global basis.

In the remainder of this presentation, we would like 1) to offer some insight into the possible biological origins of variation at production level, 2) describe how more precise management and integration of available technologies will allow for increased efficiencies in pork production and 3) to pride examples of the opportunities to produce differentiated products in totally integrated systems that provide a competitive advantage.

2. Origins of variation in grow-finish performance

In domestic species like the pig, the number of offspring born is an important economic trait, and the components of litter size (ovulation rate, embryonic survival and uterine capacity) responsive to genetic selection are well established (Johnson et al., 1985). However, as selection for ovulation rate has been associated with selection against early embryonic survival, and because birth weight decreases as litter size increases, selection for uterine capacity seems to be the most productive approach in genetic selection programs (Johnson et al., 1999). A study of associations among within-litter variation in birth weight and pre-weaning survival and weight gain, also led to the conclusion that selection for increased litter size that results in more low-birth-weight piglets may not be beneficial, unless measures are taken to improve the survival of the low-birth-weight offspring. Thus, the developmental competence of the pigs born, as well as the size of the litter, need critical consideration.

Existing literature that indicates that the variation in growth performance after birth may be largely determined, and essentially pre-programmed, during fetal development in the uterus. Furthermore, it is likely that these pre-programmed limitations in growth performance will only finally express themselves in the late grower / early finisher stage of production. Indeed, differences in fetal development that will likely affect postnatal growth performance can even be present without associated differences in birth weight. Thus sorting pigs by weight at the nursery and grower stages will not resolve the variation in growth performance that is still an inherent characteristic of particular pigs or litters. Thus we face the conundrum that 13 pigs born in different litters, with the same average birthweight, may originate from very different sized litters in utero, and this will pre-program these two litters to have very different postnatal growth potential.

3. Uterine capacity as the ultimate limitation on litter size.

The concept of uterine capacity was established using different experimental approaches to study effects of uterine crowding in the pig it is generally accepted that when the number of embryos exceeded 14, intrauterine crowding is a limiting factor for litter size born (Dziuk, 1968). Interestingly, in the context of variation in development in utero, the concept has been advanced that mechanisms promoting competition among embryos in the pre-implantation period will act to reduce within-litter variation in development by selectively removing the least developed embryos (van der Lende et al., 1990). Nevertheless, the more recent results of Père et al. (1997) confirm that, even in sows with "normal" ovulation rates, uterine capacity can affect both litter size and the average birth weight of the litter.

When does uterine capacity impact fetal survival and development? Day 30 to 40 of gestationis considered as the critical period when uterine capacity exerts its effects (see Vallet, 2000) and Vallet et al. (2003) suggested that fetal growth rate is less sensitive to intrauterine crowding than placental growth rate, and that an increase in placental efficiency may initially protect the developing fetus from a limitation in placental size. However, conclusions based only on a consideration of fetal weight may overlook critical effects on fetal development that are established early in gestation.

The study of within-litter variation in prenatal development suggested that the extremes of intrauterine growth retardation (IUGR) or "runting" are identified within a discrete sub-set of fetuses (Wooton et al., 1983). In subsequent studies of the association between within-litter differences in prenatal development and postnatal survival and growth, van der Lende and de Jager (1991) concluded that the lower pre-weaning growth of the runted pigs born could not be entirely explained on the basis of their lower birth weight. This suggested that IUGR or runting had a more complex effect on the developmental potential of runt pigs. Interestingly, data from the same laboratory indicated that the extent of IUGR within a litter was associated with specific patterns of embryonic survival (van der Lende et al., 1990) and the largest litters in utero generally included one or more runted fetuses. Furthermore, the data from this study supported the conclusion that within-litter variation in development was already established at the early fetal stage (day 27 to 35) of gestation.

4. Patterns of prenatal loss and developmental potential.

Pre-implantation embryonic losses are still considered to be the largest proportion of prenatal loss in the pig, with some lesser loss in the post-implantation period that will ultimately reflect uterine capacity (see review by Ashworth and Pickard, 1998). In commercial practice, this generalization likely reflects the situation in gilts in which ovulation rates of 10 to 15, associated with some degree of embryonic loss, is the primary factor limiting litter size. Weaned, first parity, sows also tend to fall into this category, because although ovulation rate may be higher (15 to 20 ovulations), many sows tend to be in a catabolic state and this decreases embryonic survival to 60 to 65% in many reported studies.

However, the dynamics of prenatal loss in existing commercial dam-lines may be changing (Foxcroft, 1997). In these populations, it appears that several generations of direct selection for litter size has produced indirectly resulted in a discrepancy between the number of conceptuses surviving to the post-implantation period and uterine capacity. As a consequence of markedly increased ovulation rates, associated with good or even modest embryonic survival in the pre-implantation period, the number of embryos surviving to the immediate post-implantation period (day 25 to 30) initially greatly exceeds uterine capacity. As a result, a substantial proportion of prenatal loss is now occurring in the post-implantation period. Even in individual gilts with 20 or more ovulations, embryonic survival rate can be 100% at day 28 of gestation (Almeida et al., 2000), whereas average first litter size is still only 10 to 12 piglets. In higher parity females, the situation may be even more extreme and mean ovulation rates of 26.6 ± 0.4 (Vonnahme et al., 2002) and 24.7 ± 0.4 (Town et al., unpublished) have been reported in commercial dam-line sows, with 15 to 20% of higher parity sows having greater than 30 ovulations. Despite relatively poor embryonic survival to day 30 (approximately 60% in both studies), numbers of conceptuses in utero at day 30 (approximately 15) still exceeded uterine capacity. Consistent with the literature reviewed earlier, uterine capacity then exerted its effects and a significant reduction in the number of conceptuses occurred by day 45 to 50 of gestation. However, as also reported in earlier literature, even this modest increased in uterine crowding around day 30 of gestation had consequences for placental development, seen as a decrease in placental volume (Almeida et al., 2000) and placental weight (Vonnahme et al., 2002).

Although the size and weight of the embryo was not seen to be affected by crowding up to day 44 of gestation, potential impacts on fetal development need careful study. If placental compensatory mechanisms are not adequate, crowding of the uterus in the early post-implantation period of gestation may affect fetal development of surviving conceptuses, in a manner analogous to IUGR. This raises important questions for both fetal and postnatal development. In the context of commercial grow-finish performance, a specific interest in effects on the development of fetal muscle fibres, which start to differentiate around day 35 of gestation in the pig, is particularly important. In contrast to situations in which the occurrence of IUGR is limited to a discrete subpopulation of “runt” fetuses (Royston et al., 1982; Wooton et al., 1983), a changing pattern of embryonic loss that results in uterine crowding in early gestation appears to produce a more uniform effect on placental development that will thus affect the development of all surviving fetuses.

5. Factors Affecting Muscle Development in the Pig.

A series of studies in the pig have demonstrated that maternal nutrition during gestation has an effect on piglet birth weight, and that low birth weight is primarily associated with a reduced number of secondary muscle fibres (Handel & Stickland, 1987; Dwyer et al., 1994). Consistent with earlier data of Hegarty and Allen (1978) indicating that runts in the litter have reduced muscle growth potential, Dwyer et al. (1993) also established a positive correlation between the total number of muscle fibres and postnatal growth potential, and that littermates with a high numbers of fibres grew faster and more efficiently than littermates with a lower number of fibres. Dwyer et al. (1994) further demonstrated that the effect of maternal nutrition occurred between 25 and 50 days of gestation, the period immediately preceding secondary muscle fibre hyperplasia.

Effects of maternal nutrition during gestation on fetal development are widely reported and this area of literature was the subject of an excellent review by Robinson et al. (1999). Furthermore, Maltin et al. (2001) extensively discussed the impact of manipulating myogenesis by various techniques in utero on subsequent muscle development. The early period of myogenesis, involving the differentiation of primary muscle fibers seems to be resistant to nutritional manipulation, whereas nutritional effects on differentiation and hyperplasia of secondary fibers have been demonstrated between day 25 to 90 of gestation.

From the perspective of using nutritional intervention and other treatments to reduce the variation in birth weight and postnatal growth within litters, it is interesting to note that the greatest reported impact of increased maternal nutrition (Dwyer et al., 1994), treatment with exogenous somatotropin during early gestation (Rehfeldt et al., 2001), and breed of sow (Ashworth et al., 1998) was on the smallest pigs within the litter. These results suggest that relative under-nutrition of the smallest fetuses in utero is the driver of low birth weight and poor postnatal growth performance. Furthermore, the early data of Widdowson (1976) showed that if limited nutrition initially results in the runting of pigs before and after birth, high subsequent feed intakes do not result in a normal development during compensatory growth, implying that some form of "fetal re-programming" had occurred in utero.

Based on the schematic representation of muscle fibre development shown in Figure 1, this led to the central hypothesis tested in a number of our recent studies, that "by detrimentally affecting placental size in early gestation, uterine crowding will also affect fetal organ development and the number and type of muscle fibres, analogous to the situation of IUGR in nutritionally challenged sows". Preliminary data from an initial experiment indicated that even when the number of conceptuses in utero does not significantly affect birth weight, "crowding" nevertheless results in measurable IUGR in the fetus (Town et al., 2002). In another study, a surgical approach was used to vary the number of fetusues developing in the uterus, and even though the uterine crowding observed was not at the level that probably occurs in existing commercial dam-line sows, a higher number of fetuses in the uterus resulted in measurable developmental changes. As shown in Figure 2, there were again effects of increasing numbers of conceptuses and fetuses in utero on placental development (Town et al., unpublished data, University of Alberta, 2003).

As shown in Table 1, among the various measures of IUGR, we were able to establish specific effects on the number of secondary muscle fibres. This provides some of the first evidence that the variation in the number of conceptuses surviving to the post-implantation period will affect not only placental but also fetal development.

Figure 1. Schematic representation of the time-course of muscle fibre development in the pig, indicating a critical window in early pregnancy when crowding effects limit placental development and set in place detrimental effects on fetal development and lifetime growth performance.

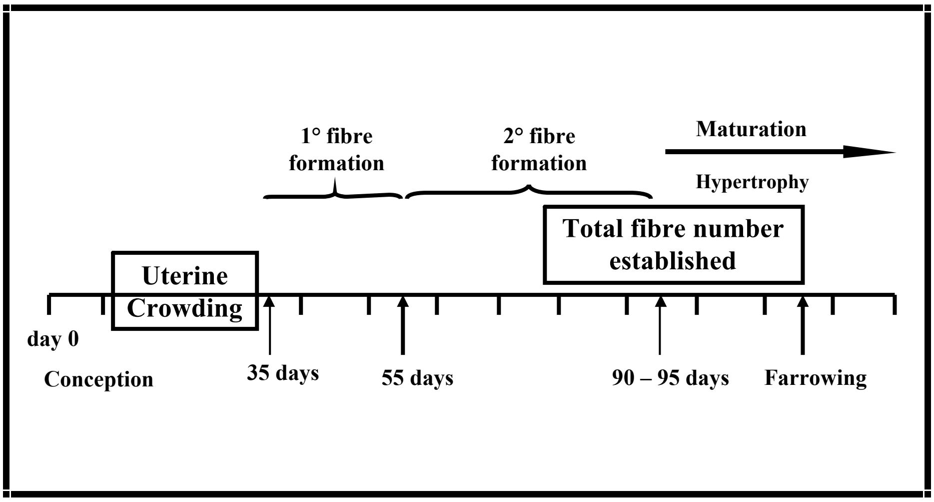
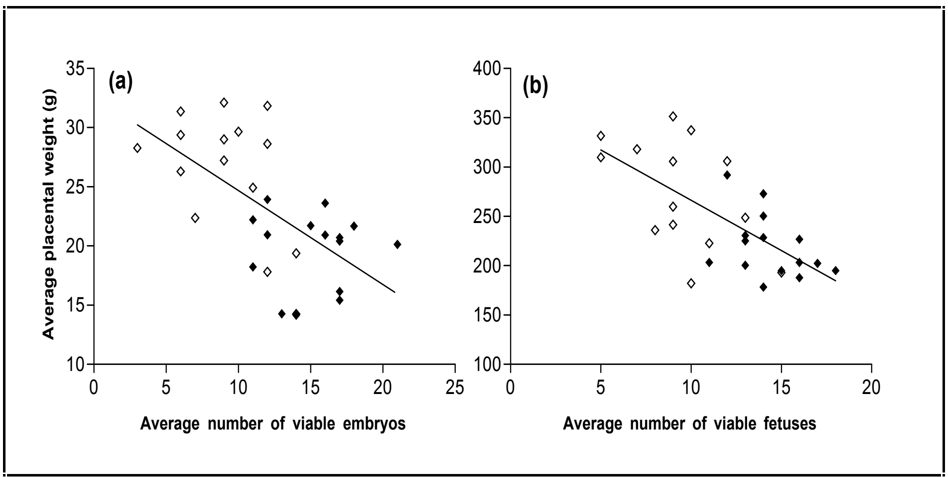


Figure 2. Correlation between average placental weight and (a) number of viable embryos at day 30 of gestation (r2 = -0.37; P = 0.0003) and (b) number of viable fetuses at day 90 of gestation (r2 = -0.45; P < 0.0001) in CTR animals (◇) and LIG animals (◆).



In the literature cited earlier, comparable effects on muscle fiber development, created by maternal under-nutrition during gestation, resulted in lifetime limitations in growth performance and muscle mass. It is thus reasonable to assume that the observed effects of embryo crowding in utero on the number of secondary muscle fibers will be associated with similar limitations in post-natal growth performance.

The extent of uterine crowding that we have managed to create in the above study, and a number of comparable studies in both gilts and higher parity sows, has been less than the crowding we predict in at least a sub-population of higher parity sows in existing commercial dam-lines. Nevertheless, it appears that we are able to demonstrate that differences in what is happening in the pre-natal period in individual females has proven consequences for the pattern of muscle fiber development. Together with the earlier literature reviewed, which suggested that muscle development in the extreme runts within a litter is also compromised, we think that these results provide a good insight into the biological origins of much of the post-natal variability in growth performance encountered in the industry.

Table 1. Muscle fibre development data (means ± SEM) for day 90 fetuses from control (CTR) and unilaterally oviduct ligated (LIG) sows (N=28).

	Treatment group	
Parameter	CTR (n=14) "Crowded"	LIG (n=14) "Non-Crowded"
Primary fibre no/mm2	29.5 ± 1.5	25.8 ± 1.3
Primary fibre CSA (µm2)	123.5 ± 5.6	130.4 ± 4.0
Secondary fibre no/mm2	678.7 ± 16.5	673.3 ± 18.6
Secondary fibre CSA (µm2)	23.1 ± 1.5	20.2 ± 0.5
Muscle weight (g)	1.25 ± 0.06a	1.47 ± 0.09b
Muscle CSA (mm2)	47.71 ± 2.85a	58.78 ± 2.65b
Number total primary fibres	1394 ± 81	1480 ± 57
Number total secondary fibres	32,691 ± 2098a	39,628 ± 2074b
Secondary:Primary fibre ratio	24.01 ± 1.49	26.80 ± 0.06

Means ± SEM within a row with different superscripts differ ($P < 0.05$)

6. Implications for variation in post-natal growth performance.

If pre-natal development makes such a profound contribution to post-natal variation in growth performance, is there any practical resolution to this problem? Perhaps one or two suggestions can be considered.

Firstly, it is likely that certain categories of sows, like high parity sows with increased ovulation rates and few problems with lactational catabolism will produce the greatest incidence of altered developmental potential due to overcrowding in utero. In the extreme situations, developmental limitations will also be associated with low birth weights, and at least this population of pigs could be designated to segregated production flows at the nursery and grow-finish stages.

The information reviewed above, also indicates that the growth potential of runt pigs within a litter will be irreversibly compromised. Therefore, simply mixing these pigs with smaller weight pigs that were not the runts in their litters, will not recognize that the developmental potential of these two sets of pigs is very different. Perhaps the best use of true runts is the barbecue market and realistically they have little potential in traditional grow-finish systems trying to compete unfairly with a succession equal weight pigs with whom they are "sorted" during the production process.

If we accept that runting and other forms of IUGR actually limits the number of muscle fibres, then it is probably unrealistic to consider that nutritional intervention can do much to alleviate this problem. The muscle mass is simply not there to produce a high level of growth performance and money spent on expensive nutritional programs to try and correct this problem may not be money well spent. However, as other data indicates that the survivability of runt pigs may also be seriously compromised, special attention to the needs of these pigs may be needed to keep them alive through the weaning and nursery stages of production.

If should be possible to identify specific dam-lines in which the balance between ovulation rate and embryonic survival, and uterine capacity, is optimal for fetal development. These selection programs will have to more effectively account for the different components of litter size, to produce a dam-line sow that has the potential to produce a uniform finishing pig throughout her reproductive lifespan.

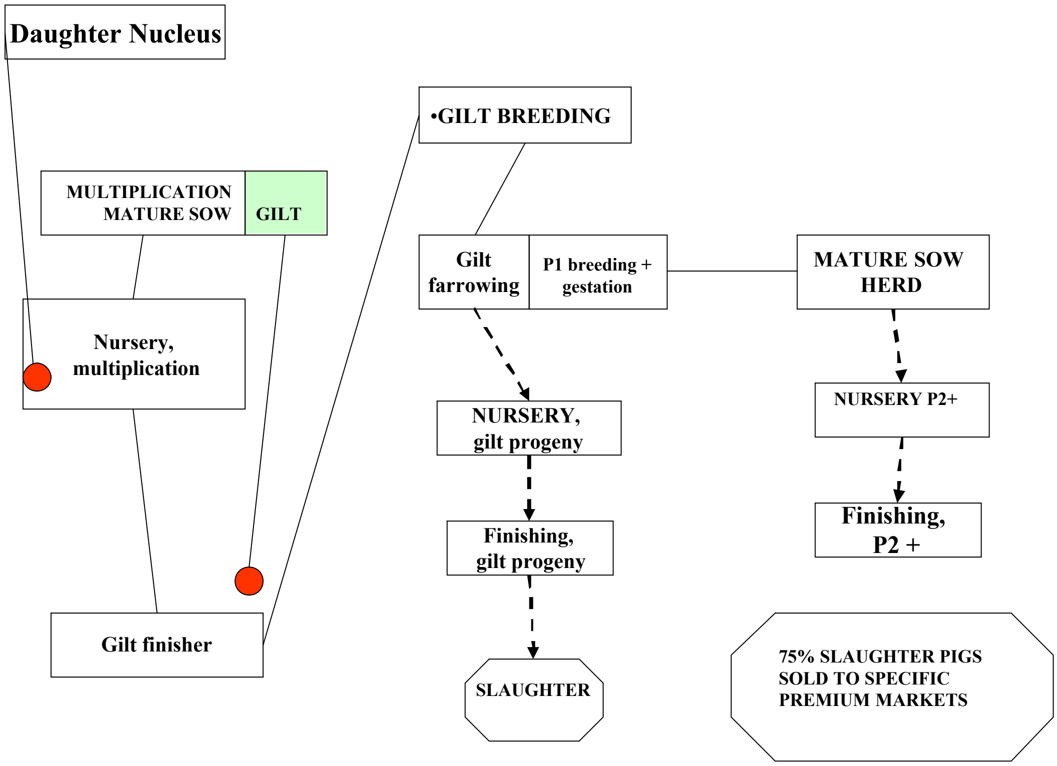
7. Development of integrated production systems.

Creating production systems that take account of known differences in potential growth performance and that seek align growth potential with production systems and specified products, provides excellent opportunities for producers to remain competitive. Increasingly, the more efficient production systems are designed to provide optimal opportunities for gilt development and segregated parity management of key replacement females. The creation of segregated management of first parity sows, has also been aligned with the designation of the offspring of these sows to different nursery and grow finish production flows. This appears to remove problems of co-mingling weaned pigs from sows of different health and immune status that destabilize the health status of the nurseries. Ultimately, if the ultimate growth potential of these offspring will clearly involve increased production costs to reach traditional finished pig markets, the marketing of these offspring at lower weights may be economically sound, and several niche markets have been developed for "suckler pigs" to specific ethnic communities.

The rebred parity one sows can then be moved to "mature" sow farms, resulting in greater health stability and more consistent performance from these key production units. The progeny of these more mature sows are recognized as having different growth potential and may be targeted at specific retail markets. Such production flows will involve use of different terminal line boars and specific nutritional programs to meet very specific product specifications. An example of this type of segregated production system is shown in Figure 3.

The success of systems like this seem to provide many opportunities for different systems of pork production that can be equally competitive in the differentiated markets of the future. Variability in production efficiency can be seem as both a challenge and an opportunity. It also provides a great opportunity to link the very best knowledge and technical ability with a wide range of production systems, and optimize the performance of each system in a predictable and cost-effective way.

Figure 3. Example of an integrated production system that captures many of the achievable advantages in production and marketing efficiency (Figure based on personal communication with Dr. Camille Moore, whose cooperation is gratefully acknowledged)



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