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Impact of genetic selection on management of boar replacement

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Abstract

Boars in an artificial insemination centre have been selected for their superior genetic potential, with ‘superior’ being defined as having traits the customer wants transmitted to his herd. The ability to meet the customers’ needs depends on the heritability of the trait, the geneticist’s success in devising a selection scheme for the trait in balance with other economically important traits, and the boar’s ability to produce sperm that can fertilise oocytes. Genetic evaluation research over the past 20 years has greatly increased the number of traits for which a boar can be selected: currently in the Canadian national program, these include age at 100 kg, backfat at 100 kg, feed efficiency, lean yield and litter size. In the near future, traits that are very likely to be added to this selection list include piglet survival, marbling, loin eye area and structure traits. In Canada, sires are ranked on two estimated breeding value (EBV) indices; one, focused on development of terminal sire lines, is based on the growth and yield traits and another, primarily focused on maternal line development, emphasises these traits and incorporates litter size.

Boars that are in Canadian AI centres because of their excellent growth traits are typically in the top 5–10% of the national population for terminal sire line index, but they may be only average or substandard for litter size. Conversely, boars selected to be in the top 5–10% for conveying such reproductive traits as litter size may only be in the top 33% for growth traits. The more offspring from a superior boar in either of these indices, the faster the population average for the trait improves. The original sire gets knocked out of the elite group, is culled and replaced by a higher ranked young boar from the now improved general population.

Although genetic superiority should govern an AI centre’s selection and culling of boars, decision-making in real life is seldom that simple. Selection criteria may be contradictory as above, or a boar with truly superior traits may be excluded because a newly-developed molecular genetics

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test determines he carries an undesirable gene such as PSS, RN or others being developed. Selection for terminal sire or maternal line traits can ignore important practical factors that affect an AI centre—boars with superior genetics may not produce good semen because skeletal or penile problems prevent ejaculation, or because sperm production is poor due to a genetic flaw, disease, or some other cause. Interestingly, selection pressure for one trait may inadvertently select for a trait that is linked but whose linkage is unrecognised, and such unintentionally selected genes could benefit, harm, or have no effect on production traits.

An AI centre serving a variety of customers must select boars in anticipation of their customers' needs (including new, foreign and niche markets). A centre should also review its genetic evaluation results and progeny records, both to critique its own selection success and to try to detect unexpected linkages. Finally, an AI centre needs to predict its own future, selecting not just for production traits for the swine producer, but also for factors that enhance the centre's efficiency including boar conformation and temperament, and sperm quantity, quality and hardiness. Can we select for efficiency? Our colleagues in dairy cattle AI evaluate bull performance—should the swine industry consider evaluation of male fertility traits?

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1. Introduction

Boars in an artificial insemination (AI) centre must produce semen that will sire pigs that the ultimate consumer will buy. Today, most consumers want pigs for meat, replacement gilts, or herd sires; niche markets exist for leather, sport, research and pets. Quantitative genetics can select boars with high genetic potential to produce offspring to meet these specialized markets, and these boars ought to be continually replaced by those with more saleable genetics. Tomorrow's saleable genetics may reflect a change in these traditional markets and/or the development of new markets for 'designer' transgenic pigs carrying human genes in their organs for xenotransplants or with commercial products in their semen (spidersilk, antibiotics, etc.) or, depending on consumer acceptance, improved commercial traits. Molecular genetics and reproductive technologies will initially develop such animals, but economics will dictate that they are propagated by classical breeding methods only after the gene is stabilized in the population (the initial animals are hemizygous and retention of the transgene is not guaranteed).

Since most pigs raised today provide meat for human consumption, the boars in today's AI studs generally are selected for their genetic potential to produce offspring that grow quickly and efficiently, and have commercially desirable meat qualities (with the definition of 'desirable' differing for different human tastes). Quick and efficient growth depends on genes for muscle fiber production, maximal feed efficiency and structural soundness, and is enhanced when females frequently bear and raise large healthy litters. Of course, each stud also has to know what their customers want, and so must select boars with the traits to meet those needs. This paper will: (a) briefly review current optimum genetic selection procedures and how an AI stud can best manage their selection program; (b) look at traits that may be selected for in the future; and (c) examine the implications of genetic selection on the day-to-day handling of boars in an AI station.

2. Contemporary genetic selection

2.1. Selection methods

Selection practices for AI boars are similar throughout the global swine industry and are universally based on genetic evaluations for economically important traits. Boars are selected on traits of primary economic importance like growth rate or age at a specific weight, fatness and productivity of their daughters. In Canada, swine breeders may voluntarily participate in a national improvement program. This program records phenotypic performance and pedigree information, which is used to compute genetic evaluations expressed as estimated breeding values (EBV) for a number of economically important traits. The EBV is based on Best Linear Unbiased Procedure, and many countries utilize similar systems.

Virtually all of the small breeders in Canada without access to their own EBV calculations use this national program as it not only provides information on which to base selection decisions but also provides a national ranking that compares an individual herd to the national performance level. These EBV are combined into two different overall indices to rank individual boars and gilts on their suitability for producing fast efficient growth in their offspring (sire line index) or for producing reasonable and efficient growth along with prolificacy (dam line index). These indices are computed by combining EBV with economic values appropriate for the Canadian swine industry to rank animals against a market endpoint [1]. AI units wishing to access boars from these breeders' herds or AI units owned by individual or allied breeders have these standardized indices and the component trait EBV available to compare boars across herds and regional boundaries.

Breeding companies follow the same general approach by measuring phenotypes and computing EBV, but frequently they will also compute specialized indices that reflect their product line focus, market niche or the economic picture of the market their genetics is designed to supply.

The important aspect in selecting a boar is not his actual EBV but his relative ranking compared to other individuals within a population. Virtually all boars in Canadian AI centres are in the top 5% of the Canadian population for their trait(s) of interest. While there are methods to compare individuals across countries to account for differences in trait definitions, units, calculation subtleties, range of EBV, etc., this is not used much in swine.

2.2. Boar selection and replacement

Boars selected on the basis of their EBV index are then screened for additional factors affecting their suitability for AI, including conformation (e.g. feet and legs), defects (e.g. malformed teats), deleterious alleles (e.g. RN), herd health status, genetic and product-line diversity within the unit, customer preference and local market conditions. The method of screening varies by AI unit but normally includes a review of the EBV and any available test results for specific genes, a visual inspection of the boar and an evaluation of the unit's specific product line and direction. Boar selection decisions are also tied to boar

replacement decisions. For maximum genetic progress in economically important traits, the theory states that the focus should remain on selecting boars on EBV indices, after the screening mentioned above and with additional factors used to decide among boars of close to equal merit.

The process for deciding to replace a boar is equally diverse across AI units and depends largely upon the needs and demands of each unit's client base. Boars are generally replaced when a young boar with better EBV and/or index values is available. As lamented recently by others [2,3], there is a paucity of published results from well-designed studies about factors other than EBV that do, and/or should guide the manager of today's swine AI studs in culling and selecting replacement boars. A brief survey in 2003 of 7 AI units in North America and Europe revealed that 20–45% of boars are replaced when a young boar of higher genetic merit is available (Table 1). Replacement rates were variable, but generally, all boars were replaced before their fourth birthday unless they were truly exceptional—only one AI unit reported keeping one, outstanding, boar to 6 years of age. The incidence of boars replaced for semen quality and production problems was variable but constituted a significant proportion of the culled population; this involuntary culling obviously interferes with the selection program designed by the geneticists for the unit. The management of the AI unit develops selection programs in response to market demands, which necessarily vary with the purpose of the unit. Genetic progress, genetic diversity, meeting customer needs for product characteristics and the cost of purchasing replacements (including housing capacity of the stud) are all factors in the decision process.

2.3. Traits considered for selection

2.3.1. Current traits

In the Canadian national system, traits currently evaluated include growth rate (days to 100 kg), back fat (loin fat depth at 100 kg measured ultrasonically), feed efficiency (estimated kg of feed per kg of gain), lean yield (estimated lean tissue content of the carcass), loin depth (depth of the *longissimus dorsi* muscle measured ultrasonically), loin eye area (estimated area of the exposed face of the *longissimus dorsi* muscle in a ribbed carcass) and litter size (total number born or number born alive). Accuracy of EBV for the growth and predicted carcass traits is generally high as boars will all have their own performance information as well as the performance of their littermates and other relatives incorporated into the EBV. Litter size, however, is low in heritability (about 10% [4]) and is

Table 1
Survey results of AI units in Canada, Denmark, The Netherlands, Norway and USA

| Unit(s) capacity (# boars) | Annual % replaced | Reasons for replacing boars (annual %) | | | | |
|-------------------------------|----------------------|--|---------------|--------|--------------------|-------|
| | | Genetics | Semen quality | Libido | Physical soundness | Other |
| 164–2000 | 50–145% | 20–45% | 10–30% | 1–21% | 13–60 | 10–20 |

Breeds of boars differed within and among units [Danbred, Duroc, Genetiporc, Hampshire, Landrace (various types), PIC, Yorkshire and various crossbreds]. Respondents, some of whom provided combined data from several different units, indicated that different breeds of boars had differing rates of culling for both genetic and non-genetic reasons. All values are the range reported by all respondents.

not measured on the boar himself. Until a boar accumulates data on the litter size produced by a number of his daughters, this EBV will be lower in accuracy than those for the growth traits. Selection is therefore most effective on growth and fatness traits as evidenced by recent genetic trends [1].

In addition to quantitative trait selection, specific genetic markers are used in selection programs [5]. The RYR1 (PSS) gene and the RN gene are two well-known examples of genetic tests for deleterious alleles affecting the quality of the meat of pigs carrying one or two copies of the ‘bad’ allele. In both these cases, the ‘bad’ allele is associated with an increase in lean yield of the carcass but a decrease in meat quality that shows up as pale, soft and exudative pork. Breeding companies may have proprietary marker allele tests of their own for alleles that contribute to or detract from the performance of individuals with those alleles (e.g. PICmarqTM for PIC, Babcoq Genetics Inc., Monsanto/Dekalb Choice Genetics [3]).

2.3.2. Potential traits

The Canadian national system is currently developing a number of new trait EBV for consideration in selection indices; meat color, marbling or intramuscular fat and conformation [1]. Meat color, measured either with an instrument producing three values describing the color or with a set of standard samples against which a cut of meat is compared, is of interest for selecting boars as sires of pigs for niche markets where darker meat color brings an increased return. Intramuscular or marbling fat measured by real-time ultrasound or by visually scoring a cross-section of the *longissimus dorsi* muscle post-slaughter is of interest to some consumers due to the increase in juiciness and taste associated with an increase in the percentage of intramuscular or marbling fat in the meat. Conformation is scored visually and pigs are rated for strength and shape of their feet and legs, arrangement and number of teats and other characteristics that affect their productive ability and potential herd life [6]; National Swine Improvement Federation (1996) [*Guidelines for uniform swine improvement programs*]. Breeding companies and other organizations with their own performance system may monitor these traits or perhaps other traits of greater importance to their individual product development program. Selection indices may also be developed for a number of other traits, including: (1) color of skin, hair and/or hair root to satisfy markets where dark hair roots in the skin are not preferred; (2) body length of increased proportion of loin in the carcass; (3) appetite in order to influence efficiency of growth rate or maternal performance; (4) temperament and/or mothering ability to incorporate other factors influencing the size of litter at weaning; (5) fatness at higher or lower carcass weights and many others.

One of the challenges of incorporating molecular genetic markers in the selection process is deciding upon the optimal combination of selection based on markers (marker-assisted selection, MAS) and conventional selection on EBV. AI units have the additional complication of factoring in the other aspects of boar selection necessary for AI. Theory abounds for the optimal combination of MAS and conventional EBV selection [7,8]. The goal is to seek a balance between emphasizing the marker information and the EBV information. There is often a tendency, as with any new technology, to emphasize the marker information too much. Over-emphasizing marker allele status in selection and boar

purchase decisions can result in loss of selection efficiency for economically important traits, so that less progress is made than with selection on EBV alone.

Modern reproductive technologies and gene manipulation tools may well play a prominent role in developing the pigs of the future, creating a few, extraordinarily expensive and valuable founder animals. Testicular transplants [9], intra-cytoplasmic sperm injection, in vitro fertilization, and embryo transplants are all tools that can be used to promote propagation and decrease generation intervals of such ‘designer’ animals [10]. These founders will then need to be propagated by careful management of sires and dams using established AI and breeding technologies. Possible examples of future porcine products are: organs with human genes for surgical xenotransplant; seminal fluid containing spidersilk, antibiotics or other commercially valuable products; meat with modified fat levels (e.g. cholesterol, fatty acids, etc.); and pigs with increased genetic resistance to disease. However, the western world’s lack of acceptance of genetically modified organisms (GMOs) as food animals clearly means that GMOs destined for a food market are unlikely to be commercially viable. Using GMOs for medical, industrial or other non-food purposes may be accepted, creating a very specialized market for these animals, and the animals will be very strictly controlled. Most of this work will be done by a few companies with strong enough financial resources to develop the product, and they will then reap the benefits.

Perhaps, the most likely scenario is continuation of the ongoing quest for existing genes in alternative breeds (like fat deposition genes in Berkshire and Tamworth, and genes increasing prolificacy in breeds like Meishan, etc.) with any successes then being moved into domestic breeds/lines using marker-assisted introgression. Marker-assisted introgression is an adaptation of marker-assisted selection in which two (or more) breeds are crossed and specific markers from one breed are tracked and fixed within the population while maintaining the characteristics of the other breed. For example, suppose breed A has a favorable marker allele at high frequency but breed B is preferred by producers and consumers. A cross of the two breeds produces the classical Mendelian ratios for the marker genotypes and individuals that carry or are homozygous for the breed A allele are selected for characteristics typical of breed B. The end result is a high frequency of the breed A allele in pigs that perform like breed B.

3. Practical implications of genetic selection on boar management in an AI centre

Regardless of a boar’s genetic potential to produce desirable offspring, he is worthless to an AI unit if he cannot produce semen. In a perfect world, boars in an AI station would only be culled when their genetics were passé, and clearly the substantial culling for other reasons (Table 1) indicates issues that the swine AI industry needs to have addressed.

3.1. Does growth rate damage semen?

Given that AI centres are culling at least some valuable selected boars because of poor semen, one question must be: is our current selection for growth and leanness actually damaging semen quality? There is not a lot of good information available on this issue,

particularly in males, and most particularly for male pigs. However, the chicken has been even more highly selected than the pig for growth rate, and may serve as a model. One recent, thorough, study did indeed look at the impact of selection for growth on male fertility [11]. Chickens were selected for five to seven generations for rate of growth (final weight—start weight/age at final weight) either over their first 14 days (roughly equivalent to weaning age for pigs) or the period from 14 to 42 days (weaning to market weight). Control lines were not selected, and had significantly lower growth rates at the end of the selection period. Both *in vitro* and *in vivo* fertility tests for the roosters found significantly poorer fertility in those males selected for rapid growth rate from 14 to 42 days, and fewer total sperm in an ejaculate [12]. Furthermore, growth rate from 14 to 42 days of age was negatively correlated, both genotypically and phenotypically, to sperm binding to the egg perivitelline membrane, a trait that is positively correlated to fertility [11]. Female pigs respond similarly [13] and taken together, the evidence clearly suggests that current selection criteria could certainly ultimately cause a reduction in porcine semen quality and fertility. Certainly factors that a manager can control, such as collection frequency [2], feed and other factors [3] will affect semen quantity and quality, but a good manager must be aware of the potential genetic basis behind poor semen and consider screening boars for relationship to boars known to be poor semen producers.

3.2. *Are semen traits heritable?*

The economic reality of an AI centre is that, primarily, a boar's productivity depends on the number of spermatozoa he produces per week, or month. Of secondary importance is his fertility, because in practice, fertility is only an issue if a reasonable number of customers complain about one boar's poor pregnancy rates or small litter sizes. Therefore, a second question is: can we select for improved semen production? Or, to put it more broadly, are semen production traits heritable?

The number of spermatozoa a boar produces per month is limited by his testicular capacity, libido and physical soundness (feet, legs, back); monthly production is affected by collection (frequency [2] and animal handling), health, season, age, feeding [3] and other factors [14,15]. Commercially important sperm quality measures (morphology, motility, longevity in extender, fertilizing ability) are affected by maturation in the male tract, collection and processing, and the dam herself. All these contributing factors make it difficult to determine if there is a genetic basis for poor semen, and so it is extremely easy for such genes to be maintained and even deliberately or unintentionally propagated in the breeding herd, if the male carrying them has good production traits.

3.2.1. *Heritability of fertility*

Farrowing rate and litter size are of enormous commercial importance and, while linked, are arguably best examined separately. Unfortunately, there is a dearth of conclusive studies on the boar's impact on these important economic measures, and little more on males from other species.

Very little is known about boars' impact on farrowing rate, so mostly we must draw implications from other species. A whole line of ducks was successfully selected for an increased number of fertile eggs [16], but the authors assumed they were improving the

female side. They did not look at any of the characteristics of the drakes in their selected lines, although they did use those selected line drakes as sires. So fertility can be selected for, but do males contribute? Of 26 bulls used in a controlled AI study inseminating cows in three herds, those whose semen was positive for a fertility-associated antigen resulted in a significantly improved pregnancy rate (66% versus 50% for controls, $p < 0.005$ [17]). Clearly, males in a monotocous species can contribute to fertility, but what about in polytocous species? Different boars produced apparently good-quality semen which, used in AI under controlled conditions, altered farrowing rates: the average farrowing rate for three boars was 75%, while a fourth boar's was 33% [18]. However, no definitive tests were undertaken to compare the boars, so at best this is an indication of possible male genetic impact on porcine pregnancy rates. Of potentially crucial importance are the findings coming from studies using knock-out mice. An excellent recent review of genes related to mammalian fertility [19] includes the activin receptor II gene: males lacking this gene are fertile, although they reach puberty late and with smaller-than-normal testes, but females are completely infertile. Certainly, a boar with these traits normally would be culled, but if he were a true 'genetic giant' in production traits, he might indeed be used and could therefore be producing infertile daughters and carrier sons. Of greater concern is the estrogen receptor beta. Male mice lacking the estrogen receptor beta (ESR) are phenotypically normal and completely fertile, although their prostates do enlarge in later life [20]. However, females lacking this receptor are subfertile, clearly implying that an apparently normal fertile male can be transmitting a genetic cause of subfertility to his female offspring. Taken all together, these studies provide ample evidence to believe there is a male genetic influence on pregnancy rate, which warrants definitive study in pigs. Large commercial swine units using AI could, on their own or in collaboration with research institutes, carry out such valuable studies.

Evidence does exist, in pigs, for genetic impact on litter size. Certainly, female pigs can be selected for improved litter size [21], but males also contribute. Reciprocal translocations occur when different chromosomes exchange pieces, and subsequent segregation during meiosis produces gametes that can be balanced or unbalanced with respect to the chromosomes carrying the translocations, with the unbalanced gametes carrying a chromatid that is either too long or too short. If such a spermatozoon penetrates an egg, the unbalanced chromatid cannot pair properly with the female partner chromatid, resulting in early embryonic death and therefore a smaller litter. Numerous such translocations have been identified in boars [22,23], and a Finnish York boar carrying such a translocation produced an average of two less pigs per litter than the breed average [23]. Furthermore, although the offspring that receive the unbalanced chromosome die, half of the living offspring carry the balanced translocation, and these offspring are subfertile: 16 daughters of the York boar were bred, producing 9.35 pigs per litter in contrast to the breed average for gilts of 10.3. Although in this case the originating translocation apparently resulted from a spontaneous translocation, the problem can clearly be perpetuated in subsequent generations. It has been strongly recommended that AI stations should not admit boars with genetic abnormalities [24], and Makinen et al. [23] report that France now tests all boars entering an AI station cytogenetically, and Sweden is considering it.

3.2.2. Heritability of semen productivity

The semen traits that affect AI centre profitability are volume, sperm concentration and gross sperm morphology. Semen volume and sperm concentration have been thought to be heritable traits, but estimates of heritabilities [25,26] and repeatabilities [26,27] for these traits varied widely. In bulls, heritability estimates range from extremely low to high (0.086–0.65 [28,29]), with estimates of the repeatability of semen traits being moderate to high (0.24–0.71 [30,31]). When we evaluated the records of semen collected commercially from 198 North American Holsteins over one year (>5000 ejaculates), we found that semen volume, sperm concentration and total sperm per ejaculate were all highly heritable in mature bulls (0.44, 0.36, 0.54) with high repeatability as well [14]. Interestingly, French Montbéliard bulls, a totally unrelated breed, also had highly heritable semen volume (0.49), although not sperm concentration [15]. Overall, then, there is strong evidence suggesting that we can select males to produce more sperm in an AI setting, and certainly the swine AI centres collect the appropriate data to determine which, if any, breeds could best profit from this approach. Again, a carefully designed study analyzing the wealth of data available in large boar studs for heritability and correlations of boar sperm characteristics and fertility would be of immense value to the swine AI industry.

4. The future of selection and boar management

- EBV for commercially important traits, while still the mainstay of selection, must not be the sole criteria, as they could ignore, and possibly select for, poor semen production.
- Phenotypic selection through culling for poor semen quality and quantity must be continued with increased vigilance, and offspring or relatives of boars with poor semen quality should be scrutinized closely before being allowed to enter an AI stud.
- Use of QTLs will improve selection efficiency but could be negatively correlated with male fertility. Fertility databases, and systems to evaluate non-return rate or other fertility-associated traits, must be established to provide a selection tool to avoid such a problem [32].

Semen and boar conformation traits of commercial importance to AI units should be the subject of intensive research by national or international selection experts to determine heritability, and permit addition of these ‘profitability traits’ into boar selection indices.

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