Historical and futuristic developments in bovine semen technology

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Implications This review summarizes key milestones and individuals involved in the evolution of our current knowledge on sperm biology and semen technologies associated with artificial insemination in cattle.

Abstract Up to the eighteenth century, the prevailing view of reproduction, or 'generation' as it was referred to, was that organisms develop from miniatures of themselves, termed preformation. The alternative theory, epigenesis, proposed that the structure of an animal emerges gradually from a relatively formless egg. The teachings of the Ancient Greeks who argued either that both sexes each contributed 'semen' to form the embryo, or held a more male-centered view that the female merely provided fertile ground for the male seed to grow, dominated thinking until the seventeenth century, when the combined work of numerous scholars led to the theory that all female organisms, including humans, produced eggs. The sequence of events leading to the commercial use of artificial insemination (AI) date back to the discovery of sperm in 1678, although it took almost 100 years to demonstrate that sperm were the agents of fertilisation and a further 100 years for the detailed events associated with fertilisation to be elucidated. The first successful AI, carried out in the dog, dates back to 1780 while it was not until the early to mid-1900s that practical methods for AI were described in Russia. Inspired by the Russian success, the first AI cooperative was established in Denmark in 1936 and later in the U.S. in 1938. The next major advances involved development of semen extenders, addition of antibiotics to semen, and the discovery in 1949 that glycerol protected sperm during cryopreservation. Almost four decades later, the flow cytometric separation of X- and Y-bearing sperm opened a new chapter in the application of AI for cattle breeding. As we look forward today, developments in imaging sperm and breakthroughs in gene editing and stem cell technology are opening up new possibilities to manipulate reproduction in a way never thought possible by the pioneers of the past. This review highlights some of the main milestones and individuals in the history of sperm biology and the development of technologies associated with AI in cattle.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Ontology and endocrinology of the reproductive system of bulls from fetus to maturity

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Implications A good understanding of prenatal and post-natal development of the reproductive system of bulls and the factors affecting this development provides the basis for 'best practice' recommendations on the management of pregnant seedstock dams and management of young bulls through to them either, becoming herd sires or semen donors. Both prenatal and postnatal development of the reproductive system is controlled by interactions between genetic and environmental factors. Some disturbances in development may be diagnosed prior to puberty but some such as unilateral testicular hypoplasia and premature spiral deviation of the penis may not manifest until months to several years after bulls reach puberty.

Abstract This review focusses on current understanding of prenatal, prepubertal and post-pubertal development of the male reproductive system of cattle. The critical developmental events occur during the first 3 to 4 mo of gestation and the first approximately 6 to 9 mo after birth. The Wilms Tumour-1 and SRY proteins play critical roles in early development and differentiation of the fetal testis, which in turn drives gestational development of the entire male reproductive system. The hypothalamic-pituitary-gonadal axis matures earlier in the bovine fetus than other domestic species with descent of the testes into the scrotum occurring around the 4th mo of gestation. An array of congenital abnormalities affecting the reproductive system of bulls has been reported and most are considered to be heritable, although the mode of inheritance in most cases has not been fully defined. Early postnatal detection of most of these abnormalities is problematic as clinical signs are generally not expressed until after puberty. Development of genomic markers for these abnormalities would enable early culling of affected calves in seedstock herds. The postnatal early sustained increase in LH secretion cues the rapid growth of the testes in the bull calf leading to the onset of puberty. There is good evidence that both genetic and environmental factors, in particular postnatal nutrition, control or influence development and maturation of the reproductive system. For example, in *Bos taurus* genotypes which have had sustained genetic selection pressure applied for fertility, and where young bulls are managed on a moderate to high plane of nutrition puberty typically occurs at 8 to 12 months of age. However, in many *Bos indicus* genotypes where there has been little selection pressure for fertility and where young bulls are reared on a low plane of nutrition, puberty typically occurs between 15 to 17 mo. Our understanding of the control and expression of sexual behaviour in bulls is limited, particularly in *Bos indicus* genotypes.

Conclusions Despite significant advances in our understanding of the genetic control of prenatal and postnatal development of the male reproductive system, the genomic basis for many suspected heritable abnormalities has not been determined. This is important because for many of the abnormalities of the reproductive system of bulls clinical signs are only expressed after puberty (e.g unilateral testicular hypoplasia), they may spontaneously resolve (e.g rupture of a persistent frenulum during first mating), or they can only be detected by observing the bull attempting to serve repeatedly (e.g premature spiral deviation of the penis). Furthermore, in contrast to sheep, in cattle we still have only a limited understanding of the impact of environmental factors on both in-utero and longer term development and function. Finally, the major area of deficiency in our understanding of development of the reproductive system of the bulls is development and endocrine control of sexual behaviour.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Spermatogenesis in the bull

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Implication This review article focuses on the exocrine function of the testis with particular emphasis on accumulated knowledge in cattle. The information described will be useful for scientists seeking basic knowledge of bull spermatogenesis.

Abstract Spermatogenesis is a finely regulated process of germ cell multiplication and differentiation leading to the production of spermatozoa in the seminiferous tubules. Spermatogenesis can be divided into three parts: spermatocytogenesis, meiosis and spermiogenesis. During spermatocytogenesis, germ cells engage in a cycle of several mitotic divisions that increases the yield of spermatogenesis and to renew stem cells and produce spermatogonia and primary spermatocytes. Meiosis involves duplication and exchange of genetic material and two cell divisions that reduce the chromosome number and yield four haploid round spermatids. Spermiogenesis involves the differentiation of round spermatids into fully mature spermatozoa released into the lumin of seminiferous tubules. The seminiferous epithelium is composed of several generations of germ cells due to the fact that new generations of sperm cells engage in the spermatogenic process without waiting for the preceding generations to have completed their evolution and to have disappeared as spermatozoa into the lumen of the tubules. In bulls, the duration of the seminiferous epithelium cycle is 13.5 days. The total duration of spermatogenesis is 61 days, i.e. 4.5 times the duration of the cycle of the seminiferous epithelium. The spermatogenetic wave is used to describe the spatial arrangement of cell associations along the tubules. Several theories have been described to explain the renewal of spermatogonia. Depending on the model, there are 5 or 6 spermatogonial mitoses explaining the renewal of stem cells and the proliferation of spermatogonia. Daily sperm production and germ cell degeneration can be quantified from numbers of germ cells in various steps of development throughout spermatogenesis. Bulls have a lower efficiency of spermatogenesis than most species examined, but higher than that of humans.

Conclusion Spermatogenesis is a long and orderly process through which spermatozoa are produced within seminiferous tubules and is divided into spermatocytogenesis (mitosis), meiosis, and spermiogenesis (differentiation without division). Spermatocytogenesis involves mitotic cell division to increase the yield of spermatogenesis and to produce stem cells and primary spermatocytes. Spermiogenesis involves an unsurpassed example of cell differentiation in the production of a self-propelled, penetrative enzyme-containing, and male genome delivery system, spermatozoa. Germ cell degeneration occurs throughout spermatogenesis, but is greater during spermatocytogenesis and meiosis and can vary with pubertal development, age, and species. Sertoli cell number is important in determining daily production of spermatozoa in bulls as well as in other species. The reason bulls have a lower efficiency of spermatogenesis than most species, other than humans, is not clear.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

The effect of nutrition on timing of pubertal onset and subsequent fertility in the bull

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Implications This review highlights the importance of enhancing early life nutrition of bulls in order to ensure early onset of puberty and sexual maturation. We also highlight the lack of evidence for a substantial effect of dietary augmentation on advancement of sexual maturity, once calves have reached six months of age, or indeed an appreciable effect of diet *per se* on semen quality in well managed post-pubertal bulls. Therefore, cattle producers and breeding companies must ensure that young bulls receive preferential nutritional and health management from birth in order to maximise lifetime fertility and return on their investment.

Abstract The advent of genomic selection has led to increased interest within the cattle breeding industry to market semen from young bulls as early as possible. However, both the quantity and quality of such semen is dictated by the age at which these animals reach puberty. Enhancing early life plane of nutrition of the bull stimulates a complex biochemical interplay involving metabolic and neuro endocrine signalling and culminating in enhanced testicular growth and development and earlier onset of sexual maturation. Recent evidence suggests that an enhanced plane of nutrition leads to an advancement of testicular development in bulls at 18 weeks of age. However, as of yet, much of the neuronal mechanisms regulating these developmental processes remain to be elucidated in the bull. While early life nutrition clearly affects the sexual maturation process in bulls, there is little evidence for latent effects on semen traits post puberty. Equally the influence of prevailing nutritional status on the fertility of mature bulls is unclear though management practices that result in clinical or even subclinical metabolic disease can undoubtedly impact upon normal sexual function. Dietary supplements enriched with various polyunsaturated fatty acids or fortified with trace elements do not consistently affect reproductive function in the bull, certainly where animals are already adequately nourished. Further insight on how nutrition mediates the biochemical interaction between neuroendocrine and testicular processes will facilitate optimisation of nutritional regimens to optimise sexual maturation and subsequent semen production in bulls.

Conclusions Enhancing the plane of nutrition of bull calves during the first six months of life will increase gonadotropin secretion and testicular development, resulting in earlier onset of puberty. Recent evidence shows that this is likely mediated through the signalling activity of peripherally derived metabolites and metabolic hormones to neuroendocrine centres within the brain and mediated by the actions of specialised neuropeptides. This leads to enhanced gonadotrophin synthesis and secretion which in turn controls testicular development and function. Improvement of our knowledge on these complex biochemical interactions will be important for designing future nutritional regimes to hasten the onset of puberty, particularly for genetically elite young bulls. Post pubertal nutrition also plays a role in maintenance of normal semen production; however, most of these improvements are often only observed in situations where animals are already deficient in the nutrient under investigation.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Using artificial insemination vs natural service in beef herds

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Implications Artificial insemination (AI) has proven to be a reliable technology for cattle producers to improve genetic progress and control venereal diseases in their herds. However, when the AI program is not adequate to the farm conditions, it can diminish reproductive efficiency by increasing the calving to conception interval and, thus, increasing the calving interval compared to natural service (NS). Hormonal stimulation is already a consistent and well-proven strategy used to improve the reproductive performance in beef herds.

Abstract The aim of this review is to compare the performance of different reproductive programs using natural service, estrus synchronization treatment prior to natural service (timed natural breeding, TNB), artificial insemination following estrus detection, and timed artificial insemination (TAI) in beef herds. It is well known that after parturition the beef cow undergoes a period of anestrous, when they do not exhibit estrus, eliminating the opportunity to become pregnant in the early postpartum by natural mating or by AI after detection of estrus. Hormonal stimulation is already a consistent and well-proven strategy used to overcome postpartum anestrus in beef herds. Basically, hormones that normally are produced during the estrous cycle of the cow can be administered in physiological doses to induce cyclicity and to precisely synchronize follicular growth, estrus and ovulation. Furthermore, two options of mating may be used after hormonal stimulation: natural service (i.e. utilization of bull service after synchronization, referred to as timed natural breeding; TNB) and timed artificial insemination (TAI). These strategies improve the reproductive efficiency of the herds compared to natural service without estrus induction or synchronization. After the first synchronized service, the most common strategy adopted to get non-pregnant cows pregnant soon is the introduction of clean-up bulls until the end of the breeding season. However, methods to resynchronize non-pregnant cows after the first service are already well established and offer a potential tool to reduce time for subsequent inseminations. Thus, the use of these technologies enable to eliminate the use of bulls by using resynchronization programs (i.e. two, three our four sequential TAI procedures). The dissemination of efficient reproductive procedures, such as TNB, TAI and Resynch programs, either isolated or in combination, enables the production of a greater quantity (obtaining increased pregnancy rates early in the breeding season) and quality (maximization of the use of AI with superior genetic sires) of beef calves. These technologies can contribute to improve the production efficiency, and consequently, improve livestock profitability.

Summary and conclusions

The high incidence of postpartum anestrus and the low efficiency, the prolonged time and great effort required to accomplish estrus detection have limited reproductive efficiency, the widespread application and the success of AI on beef farms. This condition has to be taken into consideration when deciding to begin an AI program. However, the dissemination of efficient reproductive procedures, such as TNB, TAI and Resynch programs described herein, either alone or in combination, enables the production of a greater quantity (getting high pregnancy rate early in the breeding season) and quality (maximization of the use of AI with superior genetic sires) of beef calves. These technologies can contribute to improve the production efficiency, and consequently, improve livestock profitability.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Understanding the causes of variation in reproductive wastage among bulls

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Implications A substantial number of bulls whose semen passes the post-thaw quality control checks in artificial insemination centres have reduced fertility in the field. While this is undoubtedly multifactorial, the purpose of this review is to attempt to identify where in the sequence of events, sperm from low fertility bulls compromise the establishment of pregnancy. Understanding this will aid in the development of improved strategies for the early detection of bull subfertility and/or its amelioration.

Abstract The ability to predict the fertility of bulls before semen is released into the field has been a long term objective of the animal breeding industry. However, the recent shift in the dairy industry towards the intensive use of young genomically selected bulls has increased its urgency. Such bulls, which are often in the highest demand, are frequently only used intensively for one season and consequently there is limited time to track their field fertility. A more pressing issue is that they produce fewer sperm per ejaculate than mature bulls and therefore there is a need to reduce the sperm number per straw to the minimum required without a concomitant reduction in fertility. However, as individual bulls vary in the minimum number of sperm required to achieve their maximum fertility, this cannot be currently achieved without extensive field-testing. While an *in vitro* semen quality test, or combination of tests, which can accurately and consistently determine a bull's fertility and the optimum sperm number required represent the 'holy grail' in terms of semen assessment, this has not been achieved to date. Understanding the underlying causes of variation in bull fertility is a key prerequisite to achieving this goal. In this review, we consider the reliability of sire conception rate estimates and then consider where along the pregnancy establishment axis the variation in reproductive loss between bulls occurs. We discuss the etiology of these deficiencies in sperm function and propose avenues for future investigation.

Future directions of research directed at understanding the etiology of idiopathic bull fertility

Male fertility has received far less attention in comparison to female fertility yet it is undoubtedly complex and definitely multifactorial. Despite many positive findings, the small numbers of bulls and, in some cases, an unreliable fertility phenotype due to insufficient insemination records for individual bulls as well as issues around sperm number used make interpretation of the findings of many studies challenging and sometimes unrepeatable when applied to different datasets. Despite this, it is now clear that that the sperm deliver not only DNA but also RNA and signaling factors to the oocyte at fertilisation. The most fruitful avenues of further investigation would appear to be around the differences among bulls in the kinetics of sperm penetration as well as completion of the first cell cycle and of the first mitotic cleavage after fertilisation. Embryos that cleave first are most likely to successfully reach the blastocyst stage and the quality of these embryos is superior at the preimplantation stage than later developing embryos. The pathophysiology of delayed cleavage may reside with the non-coding RNAs and or alterations in epigenetic signatures within the sperm which are most likely to be altered during testicular development or by epididymal modifications. An in-depth examination of these factors may shed new light on the cross-talk between bovine sperm and the early stages of embryo development; and importantly how this may be perturbed in bulls of low fertility. Future studies will no doubt take advantage of recent advances in high-throughput techniques to study DNA, RNAs, proteins, lipids, glycans and metabolites in combination. These 'OMICS'-based technologies have increased our capacity to study new and novel aspects of sperm function and to get a broader view of these complex biological systems. They hold the main advantage of providing large volumes of information at relatively low cost and recent advances in bioinformatics enable the analysis and interpretation of large datasets in a more integrated systems biology approach.

Like so many studies thus far, these technologies will undoubtedly produce lists of biomarkers that are different between bulls of varying fertility. The major challenge then is to define which ones are physiologically important. For this, we need novel functional approaches comprising of both *in vitro* and *in vivo* methods. However, as outlined earlier in this review, before we go down this path we must be cognisant of the limitations of sire fertility estimates especially when inseminations are performed with high numbers of sperm. Then, we should ensure experiments are sufficiently powered with bulls across a wide range of the fertility spectrum in the quest to identify the reasons for the variation in SCR.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Integrating a semen quality control program and sire fertility at a large artificial insemination organization

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Implications Responsible AI organizations strive to ensure that semen sold has the potential to achieve acceptable levels of fertility when used in herds of fertile, adequately-managed cows and heifers. Accordingly, many AI studs implement extensive quality control programs to increase the likelihood of selling highly fertile products. Successful quality control programs use data obtained from a variety of semen bioassays, as well as fertility data, to make data-driven, objective decisions regarding semen processing and sales. The future of semen quality control will be driven by advances in the technology used to analyze semen and our ability to correlate these tests to fertility

Abstract The technology available to assess sperm population characteristics has advanced greatly in recent years. Large artificial insemination (AI) organizations that sell bovine semen utilize many of these technologies not only for novel research purposes, but also to make decisions regarding whether to sell or discard the product. Within an AI organization, the acquisition, interpretation, and utilization of semen quality data is often performed by a quality control department. In general, quality control decisions regarding semen sales are often founded on the linkages established between semen quality and field fertility. While no one individual sperm bioassay has been successful in predicting sire fertility, many correlations to various *in vivo* fertility measures have been reported. The most powerful techniques currently available to evaluate semen are high-throughput and include computer-assisted sperm analysis (CASA) and various flow cytometric analyses that quantify attributes of fluorescently stained cells. However, all techniques measuring biological parameters are subject to the principles of precision, accuracy, and repeatability. Understanding the limitations of repeatability in laboratory analyses is important in a quality control and quality assurance program. Hence, AI organizations that acquire sizeable data sets pertaining to sperm quality and sire fertility are well-positioned to examine and comment on data collection and interpretation. This is especially true for sire fertility, where the population of AI sires has been highly selected for fertility. In the December 2017 Sire Conception Rate report by the Council on Dairy Cattle Breeding, 93% of all Holstein sires (n = 2 062) possessed fertility deviations within 3% of the breed average. Regardless of the reporting system, estimates of sire fertility should be based on an appropriate number of services per sire. Many users impose unrealistic expectations of the predictive value of these assessments due to a lack of understanding for the inherent lack of precision in binomial data gathered from field sources. Basic statistical principles warn us of the importance of experimental design, balanced treatments, sampling bias, appropriate models, and appropriate interpretation of results with consideration for sample size and statistical power. Overall, this review seeks to describe and connect the use of sperm *in vitro* bioassays, the reporting of AI sire fertility, and the management decisions surrounding the implementation of a semen quality control program.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Semen handling, time of insemination and insemination technique in cattle

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Implications Handling of semen, particularly the 0.25 ml straw, is critically important. Thawed semen needs to be protected from cold and heat shocks and an inseminated within 6-8 minutes of thawing. Uterine horn insemination give a modest improvement in conceptions rates particularly in situations where conception rates are low following uterine body inseminations. Because many of the studies that evaluated heterospermic insemination were conducted in the era of fresh semen and / or lacked adequate replication, it is difficult to deduce if there are real benefits from using heterospermic semen. Best conception rates are achieved when cows are inseminated from mid oestrus to a few hours after the end of oestrus.

Abstract In cattle artificial insemination plays not only a vital role in the successful establishment of pregnancy, which is a prerequisite for initiation of the subsequent lactation, but also in accelerating genetic improvement and facilitating the distribution of semen from genetically elite sires. The latter has been greatly facilitated by the ability to successfully cryopreserve semen. The objective of an insemination is to ensure that there is an adequate reservoir of competent, capacitated, motile sperm in the caudal region of the oviductal isthmus, the site of the main sperm reservoir in the cow, at the time of ovulation to ensure fertilisation. Handling of semen, particularly the 0.25 ml straw, is critically important. Thawed semen needs to be protected from cold and heat shocks and inseminated within 6-8 minutes of thawing. Uterine horn insemination give a modest improvement in conceptions rates particularly in situations where conception rates are low following uterine body inseminations. Most of the studies that evaluated heterospermic insemination were conducted on fresh semen only, and many lacked adequate replication. Consequently, it is difficult to deduce if there are real benefits from using heterospermic semen. While the interval from oestrous onset to time of ovulation would appear to be similar for cows and heifers at about 28 hours there is huge variation (standard deviations of 5-6 hours) around this average. While best conception rates are achieved when cows are inseminated from mid oestrus to a few hours after the onset of oestrus, this is difficult to achieve in practice. There is emerging evidence that having one insemination time, when all cows requiring insemination in the herd on that day are inseminated, does not compromise fertility provided insemination technique is good and the semen used is of high fertility.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Semen Sexing: current state of the art with emphasis on bovine species

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Implications Sex-sorting of semen has entered a new era with advanced biochemical techniques and high throughput machinery. This has made the technology easily accessible with the performance of the product improving continually. Coupled with genomic selection, the use of sex-sorted semen has the potential to rapidly accelerate genetic gain in all farmed species. It reduces animal wastage and allows the farmer choices on how to best improve the productive characteristics of their herds.

Abstract It is approaching three decades since the first public evidence of sex-sorting of semen. The technology has progressed considerably since then with a number of institutions and researchers collaborating to eventually bring this to application. The technical challenges have been quite substantial and in the early years the application was limited to only heifer inseminations. Comparable fertility of sex-sorted semen with conventional semen has been an aspirational benchmark for the industry for many years. Significant investment in research in the primary biology of sex-sorted sperm and associated sorting equipment ensured steady progress over the years and current methods particularly the new SexedULTRA 4M™ seems to have now mostly bridged this fertility gap. The dairy and beef industry have adopted this technology quite rapidly. Other animal industries are progressively testing it for application in their specific niches and environments. The current state of the art in the fundamentals of sex-sorting, the biology of the process as well as new developments in machinery are described in this review.

The Future It is perhaps fair to say that sexed semen has now ‘come of age”. The primary issues such as fertility and ease of availability have been mostly addressed. Incremental improvements in the sex-sorting methods and automation will further speed up the process. It is perfectly possible that one day, fertility of sex-sorted sperm could exceed the current fertility levels of conventional semen. The fact is that individual sperm cells are interrogated and the opportunity to remove the sub fertile sperm cells or alternatively choose only the most competent cells is also a possibility. Sex-sorted semen is globally traded and is now mainstream with almost every major AI company in the world offering a sexed product. While options on machinery and technology to sex-sort sperm cells may change in the future, the primary method to stain sperm cells using the Hoechst dye and a fluorescence signal to discriminate them in their sex ratio will still remain for the foreseeable future.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Applications and benefits of sexed semen in dairy and beef herds

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Implications Sex sorted semen is a revolutionary technology for cattle breeding. Greater utilisation of sexed semen can increase the efficiency of both dairy and beef production, increase farm profitability and improve environmental sustainability of cattle agriculture.

Abstract The use of sexed semen in dairy and beef cattle production provides a number of benefits at both farm and industry levels. There is an increasing demand for dairy and beef products across the globe, which will necessitate a greater focus on improving production efficiency. In dairy farming, there is surplus production of unwanted male calves. Male dairy calves increase the risk of dystocia compared with heifer calves, and as an unwanted by-product of breeding with conventional semen, they have a low economic value. Incorporating sexed semen into the breeding programme can minimise the number of unwanted male dairy calves and reduce dystocia. Sexed semen can be used to generate herd replacements and additional heifers for herd expansion at a faster rate from within the herd, thereby minimising biosecurity risks associated with bringing in animals from different herds. Furthermore, the use of sexed semen can increase herd genetic gain compared with use of non-sorted semen. In dairy herds, a sustainable breeding strategy could combine usage of sexed semen to generate replacements only, and usage of beef semen on all dams that are not suitable for generating replacements. This results in increased genetic gain in dairy herd, increased value of beef output from the dairy herd, and reduced greenhouse gas emissions from beef. It is important to note, however, that even a small decrease in fertility of sexed semen relative to conventional semen can negate much of the economic benefit. A high fertility sexed semen product has the potential to accelerate herd expansion, minimise waste production, improve animal welfare and increase profitability compared to non-sorted conventional semen.

Conclusion The advantages of sexed semen over conventional semen are numerous and varied. The key criterion of importance for the farmer is the relative conception rate achieved with sexed semen compared with conventional semen. In recent years, this fertility gap appears to have been narrowed. A high fertility sexed semen product allows much greater flexibility in the breeding management programme: diminished numbers of low value male dairy calves thereby eliminating a potential welfare concern; greater dairy beef production; reduced GHG emissions from beef production; greater selection intensity on the dam line; reduced barriers to crossbreeding with the Jersey breed; easier heifer rearing; and improved biosecurity. Societal concerns regarding animal welfare and GHG emissions can be at least partially addressed through widespread uptake and usage of sexed semen. The advantages conferred by sexed semen must be harnessed to improve production efficiency, and provide animal protein products that are economically, socially and environmentally sustainable.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

The potential of seminal fluid mediated paternal-maternal communication to optimise pregnancy success

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Implications The utility of artificial insemination in animal agriculture has dramatically improved production due to selective breeding. As with many reproductive technologies, artificial insemination bypasses the requirement for seminal fluid as a transport medium for sperm. These technologies demonstrate that seminal fluid is not required for pregnancy; however, it is curious that seminal fluid has a substantial effect on the female reproductive tract at insemination. This article discusses the role of seminal fluid in modulating the maternal environment during early pregnancy. Recapitulation of these events during artificial insemination may further improve pregnancy outcomes and offspring performance of domestic species.

Abstract Artificial insemination has been a landmark procedure in improving animal agriculture over the past 150 years. The utility of artificial insemination has facilitated a rapid improvement in animal genetics across agricultural species, leading to improvements of growth, health and productivity in poultry, swine, equine and cattle species. The utility of artificial insemination, as with all assisted reproductive technologies side-steps thousands of years of evolution that has led to the development of physiological systems to ensure the transmission of genetics from generation to generation. The perceived manipulation of these physiological systems as a consequence of assisted reproduction are points of interest in which research could potentially improve the success of these technologies. Indeed, seminal fluid is either removed or substantially diluted when semen is prepared for artificial insemination in domestic species. While seminal fluid is not a requirement for pregnancy, could the removal of seminal fluid from the ejaculate have negative consequences on reproductive outcomes that could be improved to further the economic benefit of artificial insemination? One such potential influence of seminal fluid on reproduction stems from the question; how does the allogeneic foetus survive gestation in the face of the maternal immune system? Observation of the maternal immune system during pregnancy has noted maternal immune tolerance to paternal specific antigens; a mechanism by which the maternal immune system tolerates specific paternal antigens expressed on the foetus. In species like human or rodent, implantation occurs days after fertilisation and as such the mechanisms to establish antigen specific tolerance must be initiated very early during pregnancy. We and others propose that these mechanisms are initiated at the time of insemination when paternal antigens are first introduced to the maternal immune system. It is unclear whether such mechanisms would also be involved in domestic species, such as cattle, where implantation occurs weeks later in gestation. A new paradigm detailing the importance of paternal-maternal communication at the time of insemination is becoming evident as it relates to maternal tolerance to foetal antigen and ultimately pregnancy success.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

The epic journey of sperm through the female reproductive tract

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Implications Sperm interaction with the cow reproductive tract after semen deposition has a profound influence on pregnancy rates and provides perplexing fundamental questions that are unresolved despite considerable study. The fertilizing sperm are selected by the tract from the millions or billions of sperm deposited at mating or artificial insemination. Successful sperm interact with luminal fluid and epithelia, while evading destruction by the immune system. They respond to rheotactic, chemical and adhesive stimuli to undergo functional changes and arrive at the site of fertilization. An understanding of how these processes are coordinated can improve *in vitro* fertilization success, contraception effectiveness, sperm lifespan in the oviduct, improved semen storage, and fertility.

Abstract Millions or billions of sperm are deposited by artificial insemination or natural mating into the cow reproductive tract but only a few arrive at the site of fertilization and only one fertilizes an oocyte. The remarkable journey that successful sperm take to reach an oocyte is long and tortuous, and includes movement through viscous fluid, avoiding dead ends and hostile immune cells. The privileged collection of sperm that complete this journey must pass selection steps in the vagina, cervix, uterus, utero-tubal junction, and oviduct. In many locations in the female reproductive tract, sperm interact with the epithelium and the luminal fluid, which can affect sperm motility and function. Sperm must also be tolerated by the immune system of the female for an adequate time to allow fertilization to occur. This review emphasizes literature about cattle but also includes work in other species that emphasizes critical broad concepts. Although all parts of the female reproductive tract are reviewed, particular attention is given to the sperm destination, the oviduct.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Sperm-oocyte interactions and their implications for bull fertility, with emphasis on the ubiquitin-proteasome system

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Implications Fertilization is an intricate cascade of events that irreversibly alter the participating male and female gamete and ultimately lead to the union of paternal and maternal genomes in the zygote. Proper functioning, recycling and remodeling of gamete structures at fertilization is aided by the ubiquitin-proteasome system (UPS), the universal substrate specific protein recycling pathway present in bovine and other mammalian oocytes and spermatozoa. Research focused on the UPS-regulated aspects of the fertilization process has a potential to impact the management of bull fertility, the optimization of artificial insemination, genomic selection for production and fertility related traits, and the improvement of sperm viability after sexing and cryopreservation in cattle.

Abstract Fertilization is an intricate cascade of events that irreversibly alter the participating male and female gamete and ultimately lead to the union of paternal and maternal genomes in the zygote. Fertilization starts with sperm capacitation within the oviductal sperm reservoir, followed by gamete recognition, sperm-zona interactions and sperm-oolemma adhesion and fusion, followed by sperm incorporation, oocyte activation, pronuclear development and embryo cleavage. At fertilization, bull spermatozoon loses its acrosome and plasma membrane components and contributes chromosomes, centriole, perinuclear theca proteins, and regulatory RNAs to the zygote. While also incorporated in oocyte cytoplasm, structures of the sperm tail, including mitochondrial sheath, axoneme, fibrous sheath and outer dense fibers are degraded and recycled. The ability of some of these sperm contributed components to give rise to functional zygotic structures and properly induce embryonic development may vary between bulls, bearing on their reproductive performance, and on the fitness, health, fertility and production traits of their offspring. Proper functioning, recycling and remodeling of gamete structures at fertilization is aided by the ubiquitin-proteasome system (UPS), the universal substrate specific protein recycling pathway present in bovine and other mammalian oocytes and spermatozoa. This review is focused on the aspects of UPS relevant to bovine fertilization and bull fertility.

Summary Gamete interactions during bovine fertilization represent an intricate mesh of remodeling, recycling and signaling that results in transformation of gamete-specific structures into zygotic components. Thus, the sperm acrosome is remodeled during capacitation causing the exposure of zona-binding ligands on the outer acrosomal membrane, and is partially lost to acrosomal exocytosis induced by the oocyte zona pellucida. The sperm head perinuclear theca dissolves in ooplasm to release oocyte activating factors, and the denuded sperm nucleus is turned into a zygotic paternal pronucleus. The reduced sperm centrosome contributes the formation of zygotic centrosomes and initiates nucleation of microtubule sperm aster necessary for maternal and paternal pronucleus apposition. Various sperm-borne RNAs may regulate early embryo development and even impose epigenetic marks. Sperm contributed paternal genome affects developmental competence of embryos and ultimately imposes heritable traits on offspring.

While some sperm accessory structures are simply recycled after fertilization as they become obsolete, the fate of sperm mitochondria is of particular interest as these have to be eliminated to promote clonal, maternal inheritance of mitochondrial genes and avoid heteroplasmy. Similarly, the regulatory influence of sperm-borne RNAs on zygotic and embryonic development warrants further investigation. Altogether, the ability of some sperm contributed structures and molecules to develop into the functional zygotic components and properly induce embryonic development may vary between bulls, bearing on their reproductive performance, and on the fitness, health, fertility and production traits of their offspring.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Testicular vascular cone development and its association with scrotal thermoregulation, semen quality and sperm production in bulls

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Implications The testicular vascular cone (TVC) is comprised of the highly coiled testicular artery surrounded by the venous pampiniform plexus. The TVC, located at the top of the testis. operates as a countercurrent heat exchanger, cooling arterial blood before it enters the testis. This role is critical, as blood flow is the primary source of heat within the testis and increased testicular temperature reduces the percentage of morphologically normal, motile and fertile sperm. Bulls with a TVC that facilitated heat transfer had better quality sperm and were more resistant to increased ambient temperatures.

Abstract Several structural and functional features keep bull testes 2 to 6 °C below body temperature, essential for production of morphologically normal, motile and fertile sperm. The testicular vascular cone (TVC), located above the testis, consists of a highly coiled testicular artery surrounded by a complex network of small veins (pampiniform plexus). The TVC functions as a counter-current heat exchanger to transfer heat from the testicular artery to the testicular vein, cooling blood before it enters the testis. Bulls with increased testicular vascular cone diameter or decreased distance between arterial and venous blood, have a greater percentage of morphologically normal sperm. Both the scrotum and testes are warmest at the origin of their blood supply (top of scrotum and bottom of testis), but they are cooler distal to that point. *In situ*, these opposing temperature gradients result in a nearly uniform testicular temperature (top to bottom), cooler than body temperature. The major source of testicular heat is blood flow, not testicular metabolism. High ambient temperatures have less deleterious effects on spermatogenesis in *Bos indicus* versus *Bos taurus* bulls; differences in TVC morphology in *B. indicus* bulls confer a better testicular blood supply and promote heat transfer. There is a longstanding paradigm that testes operate on the brink of hypoxia, increased testicular temperature does not increase blood flow, and the resulting hypoxia reduces morphologically normal and motile sperm following testicular hyperthermia. However, in recent studies in rams, either systemic hypoxia or increased testicular temperature increased testicular blood flow and there were sufficient increases in oxygen uptake to prevent tissue hypoxia. Therefore, effects of increased testicular temperature were attributed to testicular temperature *per se* and not to a secondary hypoxia. There are many causes of increased testicular temperature, including high ambient temperatures, fever, increased recumbency, high-energy diets, or experimental insulation of the scrotum or the scrotal neck. It is well known that increased testicular temperatures have adverse effects on spermatogenesis. Heat affects all germ cells and all stages of spermatogenesis, with substantial increases in temperature and/or extended intervals of increased testicular temperature having the most profound effects. Increased testicular temperature has adverse effects on percentages of motile, live and morphologically normal sperm. In particular, increased testicular temperature increases percentage of sperm with abnormal morphology, particularly head defects. Despite differences among bulls in the kind and percentage of abnormal sperm, the interval from increased testicular temperature to emergence of specific sperm defects is consistent and predictable. Scrotal surface temperatures and structural characteristics of the testis and TVC can be assessed with infrared thermography and ultrasonography, respectively.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Principles of maximizing bull semen production at genetic centers

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Implications Semen collection personnel must possess a sound understanding of bull sexual behavior in order to maximize the sperm harvest to aide their organizations to compete in today's global marketplace. Testicular capacity, breed of a bull, age, physical ability, libido, and body condition are important factors that should be independently evaluated when collecting semen from bulls. Use of novel sexual stimuli and false mounting bulls are mandatory to exploit the sperm harvest. Altering collection days and ejaculation frequencies based on sperm quality, estimated daily sperm production, and tabulated daily sperm output are necessary to meet established individual bull production goals.

Abstract Knowledge of the capabilities and limitations of the reproductive capacity of bulls is vital in maximizing reproductive efficiencies. Bull semen collection guidelines established by researchers and industry personnel to maximize the sperm harvest from bulls have been evolving for more than 60 years. Today, a mature artificial insemination industry employs those strategies to meet demands. These efficient management schemes exploit the reproductive potential of each sire while minimizing the associated risk of injury to bulls and reduce associated production costs. Personnel employed by a semen producing facility must be authorized to make effective and rational decisions based on principles of bull sexual behavior and reproductive physiology. Furthermore, collection facilities must be well planned to allow for the safe presentation of novel sexual situations while affording maximum safety for employees and proper footing for bulls. Normal bulls produce and ejaculate tremendous numbers of sperm. Most bulls have a sufficient libido for routine sexual activity, but become satiated to predictable stimulus situations. Frequent changes to the novelty should allow weekly harvest of four to six ejaculates per week for most bulls. Utilizing the physiological characteristics associated with each ejaculate to establish the collection frequency of each bull, and empowering an integrated collection and laboratory staff to monitor and make adjustments to the ejaculation frequency are necessary in maximizing the sperm harvest. Young bulls can ejaculate 10 – 20 billion sperm per week, and mature bulls should ejaculate 40 – 60 billion sperm per week. Semen collection management procedures should be reviewed when bulls do not meet production goals.

Conclusion The current trend in the artificial insemination industry is to market semen from more and more young, genomic bulls. These bulls have limited sperm producing abilities due to their young age. This movement by the industry is likely to continue into the future. Therefore, it is mandatory to properly and actively manage the semen collection from bulls, but especially younger bulls. Most mature bulls can produce and ejaculate many more sperm than can be marketed. Too often, young bulls whose semen is in great demand fail to satisfy market needs in a timely manner. An aggressive approach to semen collection for finite periods followed by periods of sexual rest is the most efficient use of labor, minimizes routine sexual boredom, and results in higher quality sperm as opposed to limiting collections to a weekly event or limiting collection day ejaculates. Monitoring sperm output from each bull, addressing needs to properly sexually prepare bulls to maximize the sperm harvest, continual staff education, integrated production teams, and assessment of testicular capacity are essential for any artificial insemination organization to capitalize on the reproductive potential of genetically superior sires. Knowledge of sexual behavior of bulls, utilization of an array of stimulus situations, use of collection and ejaculation frequencies that assure maximal sperm harvest per ejaculate and a positive attitude are needed each and every day from collection personnel. Cohesive collection and processing teams, working in harmony during collection days place accountability on the employees to assure that ejaculate volume and concentration are properly represented. These valuable employees that monitor the collection process will assure the epididymal sperm reserves are adequately depleted and the sperm harvest is maximized for each bull each collection day.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Abnormalities of the bull: occurrence, diagnosis and treatment of abnormalities of the bull, including structural soundness

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Implications There are very few sterile bulls but many bulls are subfertile due to a variety of physical conditions that reduce reproductive soundness. Developmental anomalies or injuries of the penis and prepuce are seen during breeding soundness examinations or when bulls fail to achieve a satisfactory pregnancy percentage during natural breeding (Carson and Wenzel, 1995). Numerous congenital abnormalities prevent normal development that allow for breeding soundness. Many musculoskeletal abnormalities or injuries impair a bull's ability to move freely in his environment and complete coitus. Any febrile or inflammatory condition may impair normal scrotal and testicular thermoregulation and normal sperm production. Failure to achieve pregnancy in a limited breeding season results in significant economic loss for livestock owners.

Abstract Selecting bulls for reproductive soundness requires that the bull be structurally sound, free of abnormalities that impair his ability to produce adequate numbers of motile, morphologically normal spermatozoa, and be able to successfully complete coitus. This review discusses the diagnosis and etiology of abnormalities of the penis, prepuce as well as common musculoskeletal conditions that prevent normal pasture breeding soundness. A review of testicular and thermoregulation addresses the potential impact of musculoskeletal disorders on normal sperm production.

Summary Numerous physical conditions may cause subfertility in bulls. The reader is advised to seek additional resources for discussion of ocular disease, scrotal size and pathology, as well as abnormalities of the accessory sex gland that may impair fertility. Breeding bulls should be maintained with housing and nutrition that ensures optimal health and body condition. Numerous injuries and developmental or skeletal disorders may hinder the bull's ability to display libido, and maintain normal scrotal thermoregulation to ensure the production of adequate numbers of motile, normal spermatozoa and to achieve erection, intromission, and ejaculation. A thorough history and physical examination are crucial to determining causes of infertility.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

The use of bull breeding soundness evaluation to identify subfertile and infertile bulls

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Implications Efficient and economical herd management depends a great deal on maintaining a short, well-defined, calving season. If short breeding seasons are to be successful, bulls must be selected to be highly fertile. When serving capacity, physical soundness and semen quality are taken into account about 1 in 4 bulls is unsatisfactory. Breeding soundness evaluations are a useful, low-cost screening method for reducing the risk of using low fertility bulls. Our knowledge and ability to provide reliable BBSEs exceeds what we place into practice due mainly to the time and expense that the market will bear.

Abstract Efficient and economical herd management depends a great deal on maintaining a short, well-defined calving season. This requires highly fertile females and bulls. Low pregnancy rates are very noticeable, however; potentially greater economic loss may be due to delayed conception. Many studies showed that approximately 1 of every 5 bulls had inadequate semen quality, physical soundness, or both, but when evaluation of serving capacity is included about 1 in 4 bulls is unsatisfactory. Due mainly to the time and expense that the market will bear, usually only physical soundness and semen quality are evaluated. Breeding soundness evaluation is a useful, low-cost screening method for reducing the risk of using low fertility bulls. The biggest problem with breeding soundness evaluations is not our lack of knowledge or ability, but in the willingness of veterinary schools to provide adequate equipment and training in this area, a lack of diagnostic laboratories equipped to handle the more difficult cases and, most importantly, the weaknesses of human nature that result in negligent testing procedure.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Risks of disease transmission through semen in cattle

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Implications The characteristics of viral, bacterial, protozoal, and parasitic infections and infestations of cattle vary significantly. Understanding these infections allow effective control procedures that minimally impede optimal cattle production to be thoughtfully enacted

Abstract The purpose of this paper is to review scientific evidence concerning pathogens that could potentially be transmitted via bovine semen. As a result of a careful analysis of the characteristics of infections that may cause transmission of disease through semen, effective control procedures can be identified that provide minimal constraint to the introduction of new bulls into herds for natural breeding and importation of valuable novel genetics through artificial insemination. The potential for transmission through bovine semen and corresponding effective control procedures are described for bovine herpesvirus 1, bovine viral diarrhea virus, bovine leukemia virus, lumpy skin disease virus, bluetongue virus, foot-and-mouth disease virus, and Schmallenberg virus. Brief consideration is also provided regarding the potential for transmission via semen of *Tritrichomonas foetus*, *Campylobacter fetus venerealis*, *Brucella abortus*, *Leptospira* spp., *Histophilus somni*, *Ureaplasma diversum*, *Mycobacterium avium* subsp. *paratuberculosis*, *Chlamydiaceae*, *Mycobacterium bovis*, *Coxiella burnetii*, *Mycoplasma mycoides* ssp. *mycoides* and *Neospora caninum*. Thoughtful and systematic control procedures can ensure the safety of introducing new bulls and cryopreserved semen into cattle production systems.

Conclusion Based on understanding specific viral, bacterial, protozoal, and parasitic infections that may result in contamination of bovine semen, prudent and practical control measures can be effectively developed and implemented for each farm, region, state, or country. While several pathogens can potentially be transmitted through cryopreserved bovine semen, following disease control recommendations provided by the World Organization for Animal Health (OIE) and Certified Semen Services (CSS) will ensure that the risk of pathogen transmission through semen is negligible.

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https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press

Genomics of bull fertility

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Implications Male and female fertility are lowly heritable in cattle, but the reduction in generation interval achieved through the deployment of genomic selection has allowed a rapid improvement of female fertility in U.S. dairy cattle. For several logistical reasons, genetic evaluations are not widely produced for male fertility in either beef or dairy cattle. Because the genetic correlation between male and female fertility is low, little improvement in male fertility is expected as a correlated response to selection for female fertility. To maximise food production from cattle, new approaches must be developed to improve male fertility independently of female fertility.

Abstract Fertility is one of the most economically important traits in both beef and dairy cattle production; however, only female fertility is typically subjected to selection. Male and female fertility have only a small positive genetic correlation which is likely due to the existence of a relatively small number of genetic variants within each breed that cause embryonic and developmental losses. Genomic tools have been developed that allow the identification of lethal recessive loci based upon marker haplotypes. Selection against haplotypes harbouring lethal alleles in conjunction with selection to improve female fertility will result in an improvement in male fertility. Genomic selection has resulted in a 2- to 4-fold increase in the rate of genetic improvement of most dairy traits in U.S. Holstein cattle, including female fertility. Considering the rapidly increasing rate of adoption of high-throughput single nucleotide polymorphism genotyping in both the U.S. dairy and beef industries, genomic selection should be the most effective of all currently available approaches to improve male fertility. However, male fertility phenotypes are not routinely recorded in natural service mating systems and when artificial insemination is used, semen doses may be titrated to lower post-thaw progressively motile sperm numbers for high-merit and high-demand bulls. Standardisation of sperm dosages across bull studs for semen distributed from young bulls would allow the capture of sire conception rate phenotypes for young bulls that could be used to generate predictions of genetic merit for male fertility in both males and females. These data would allow genomic selection to be implemented for male fertility in addition to female fertility within the U.S. dairy industry. While the rate of use of artificial insemination is much lower within the U.S. beef industry, the adoption of sexed semen in the dairy industry has allowed dairy herds to select cows from which heifer replacements are produced and cows that are used to produce terminal crossbred bull calves sired by beef breed bulls. Capture of sire conception rate phenotypes in dairy herds utilizing sexed semen will contribute data enabling genomic selection for male fertility in beef cattle breeds. As the commercial sector of the beef industry increasingly adopts fixed-time artificial insemination, sire conception rate phenotypes can be captured to facilitate the development of estimates of genetic merit for male fertility within U.S. beef breeds.

Conclusions Male and female fertility are positively correlated but the correlation is low and genetic predictions for fertility are currently only produced for females. Genomic selection has produced dramatic increases in female fertility in a relatively short period of time in U.S. Holsteins demonstrating that a low heritability is not the sole determinant of selection response. While this improvement should also have produced a small correlated response in male fertility, this is an unsatisfactory solution considering the economic importance of fertility to cattle production and the need to increase the efficiency and quantity of animal-based food proteins world-wide.

In dairy cattle, there is an opportunity to rapidly develop genomic predictions for male fertility (in both sexes) considering the large number of genotyped animals and the availability of SCR phenotypes. However, these phenotypes should be based on inseminations made by yearling bulls in which sperm dosages have been standardised and this will require collaboration between AI organizations. In the U.S. beef industry, the majority of genetic improvement in all traits is created by selection within the registered sector. Despite the reduced use of AI relative to the dairy industry, it should similarly be possible to capture the benefits of increased rates of genotyping to develop genetic predictions for SCR. The increasing use of sexed semen to produce heifer replacements within the U.S. dairy industry also presents an opportunity for the generation of SCR data for beef bulls, since sexed male semen from beef bulls is increasingly being used to breed dairy cows that were not selected to produce heifer replacements. Scoring conception rates in dairy cows is agnostic to the breed of bulls used in AI. Finally, increasing the rate of use of AI in commercial beef herds via the use of synchronization of oestrus and ovulation to facilitate fixed-time AI of beef cows has an enormous opportunity for the collection of SCR phenotypes in beef bulls. If 10% of the commercial beef cows in the U.S. were bred by AI, the industry could collect more SCR phenotypes than are currently produced within the entire dairy industry. If genomic predictions of merit for male fertility are to be produced for both males and females, efforts should be invested to develop and evaluate models that appropriately model the effects of sex chromosome and imprinted variants.

https://doi.org/10.1017/S2040470018000092 Published online by Cambridge University Press