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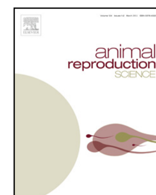

Sperm macromolecules associated with bull fertility

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ABSTRACT

Bull fertility, ability of the sperm to fertilize and activate the egg that sustain embryo development, is vitally important for effective and efficient production of cattle. Fertility is a complex trait with low heritability. Despite recent advances in genomic selection and possibility of enormous paternal benefits to profitable cattle production, there exist no reliable tests for evaluating semen quality and predicting bull fertility. This review focuses on sperm macromolecules such as transcripts, proteins and the epigenome, i.e., the functional genome that are associated with bull fertility. Generating new information in these systems is important beyond agriculture because such progress advances the fundamental science of the mammalian male gamete while at the same time introduces biotechnology into livestock production. Sperm macromolecules and epigenome markers associated with bull fertility can be used alone or in combination with the current SNP microarrays to determine sperm quality and to indicate bull fertility.

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1. Introduction

Spermatogenesis is a series of events during which spermatogonial stem cells undergo mitotic and meiotic divisions to form haploid round spermatids called spermatocytogenesis. This is followed by cellular transformation of the round spermatid into elongated mature sperm having a head and tail with all this taking place within the seminiferous tubules through the process of spermiogenesis. The cells are then released into the lumen of tubules. For the bovine bull, the entire process requires 61 days from spermatogonia to mature spermatozoa (Barth and Oko, 1989; Johnson et al., 1994).

Spermiogenesis involves major changes within the spermatid nucleus to form the head by rearrangement the chromatin structure and tightly packing of the DNA to a much smaller volume to fit in the sperm head (Ward and Coffey, 1991). The packaging of the DNA is a process whereby the somatic cell histones are replaced with sperm specific protamines that are rich in arginine and cysteine that form the inter- and intra-molecular covalent disulfate bonds between protamines (Ballhorn et al., 1987; Ward and Coffey, 1991). This results in highly condensed DNA and stabilized chromatin thereby making the paternal genome inaccessible to potential nucleases and mutagens present in the environment (Oliva, 2006).

In mammals, two types of protamines have been identified. While protamine 1 (PRM1) has been detected in all mammalian species including bull sperm (Balhorn et al., 1987; Maier et al., 1990), protamine 2 (PRM2) is only detectable in some mammalian species including human and mouse (Mengual et al., 2003; Oliva, 2006; Balhorn, 2007). Following spermiogenesis, sperm are released into the lumen of seminiferous tubules and transported to the epididymis for further physiological and morphological maturation for the sperm to acquire the ability to penetrate, and activate the oocyte and then contribute to extended embryo development (Johnson et al., 1994; Oliva and Castillo, 2011).

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It has been shown and well known that for the last 50 years despite great improvement in milk production per cow through intensive genetic selection in dairy cattle, the efficiency of reproduction has been declining due to decreasing fertility (Royal et al., 2000; Lucy, 2001). Fertility is the most important factor affecting reproductive efficiency and economic sustainability of the production of cattle. Although artificial insemination (AI) is a very successful biotechnology for cattle, the AI industry and dairy farmers are still facing major challenges associated with both male and female infertility.

Although sufficient quantity and quality of sperm may be put into breeding AI doses, there still exists significant fertility differences among bulls. This fertility variation, a prime influence limiting efficient reproduction of cattle, is regulated by "compensable" and "non-compensable" factors. Improved fertility bulls having compensable defects related to sperm viability, such as motility and acrosome integrity, can be achieved by increasing the number of spermatozoa deposited in the cow's reproductive tract. However, it may not be possible for bulls afflicted with non-compensable defects to ever demonstrate adequate zygotic, embryonic or fetal development. These defects result from molecular or genetic, functional genomic attributes of the sperm (DeJarnette et al., 2004; Saacke, 2008; Peddinti et al., 2008; Blaschek et al., 2011).

Over recent decades researchers have attempted to identify semen quality parameters that help predict sire fertility. A review of the literature indicates that no single laboratory assay can reliably predict the highest fertility bulls or their semen prior to breeding (Rodríguez-Martínez, 2003; Gillan et al., 2008). This is important because objective criteria and their specific effects on fertility are needed for culling ejaculates, as well as for understanding causes of poor quality semen. Past research results show that for the conventional way of exploring this area that semen analysis methods used were subjective, and sample sizes were small. Additionally, sire fertility was estimated relatively inaccurately (DeJarnette, 2010).

Currently, the only accurate approach for measuring sire fertility is through AI breeding and confirming the live offspring pregnancy outcome which is time consuming and expensive. It has been reported that for over 90% of the AI sperm marketed the sire fertility efficiency ranges about six percentage points. In reality, it is difficult to measure "fertility" more precisely than ±2 or 3% due to many limiting factors and complexity of fertility (DeJarnette, 2010). This means that many low fertility bulls are unknowingly used to inseminate a multitude of cows until the reproductive status of sires can be established. Both dairy farmers and AI companies are aware of the problem and continuously seek the technologies to predict sire fertility more accurately in order to offer high fertility sires and sperm without sacrificing the genetic goals of their customers.

A recent trend in dairy cattle breeding is relying on genomic selection of sires and dams. For instance, in North America over 90% of the sires used are selected by their genomic superiority with the result that the generation interval becomes shorter than in traditional progeny testing programs. On one hand the AI companies are facing high replacement rates of sires in their bull stud, resulting in the collection of young sires producing subpar production efficiency i.e. quality and quantity of semen are lower than proven bulls. On the other hand, farmers are most often use young sires of unknown fertility in their herds. This causes significant economic loss to the cattle industry (Fig. 1). Today the need for molecular fertility markers in bulls is becoming more urgent than ever.

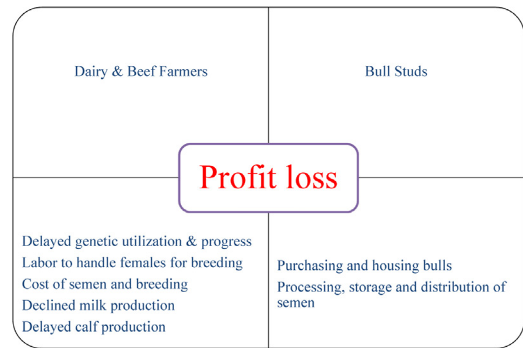

Fig. 1. Costs associated with subpar bull fertility. Accumulated costs caused by low bull fertility reduce profitability of cattle agriculture.

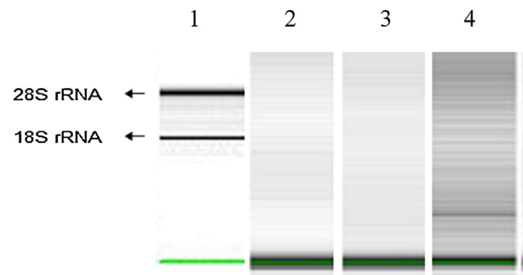

Fig. 2. Nature of sperm ribonucleic acids. RNA samples from bovine blastocysts (Lane 1) and three different bulls (Lanes 2–4) (adapted from Sagirkaya et al., 2006; Govindaraju et al., 2012a, b). Compared to embryos and somatic cells, bull spermatozoa that are transcriptionally and translationally silent do not have detectable ribosomal RNAse. Sperm mRNAs appear as degraded transcripts while the small non-coding RNAs as an intense band at the bottom of the gel.

2. Sperm ribonucleic acids (RNA) and bull fertility

Transcription from the male genome is believed to be terminated during mid-spermiogenesis, and thus mature spermatozoa do not have significant transcriptional activity. Remarkably, diverse populations of messenger RNAs (mRNA) have been detected in sperm from bulls (Gilbert et al., 2007). In contrast to somatic cells and embryos, sperm do not have detectable 18S and 28S ribosomal RNAs as the cells are also devoid of translational activity (Fig. 2). The significance of the sperm mRNA repertoire is still unknown although two probabilities exist; these transcripts are remnants of spermatogenesis and thus they reflect a mirror image of the health of genesis, and/or the paternal borne transcripts are transferred into the oocyte where they play important roles in early embryonic development.

Using DNA Microarray technology, about 3000 different transcripts are detected in the mature spermatozoa

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