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Reproductive selection of males: current and future perspectives

Reprodução seletiva em machos: perspectivas atuais e futuras

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Abstract

Appropriate selection of livestock breeding males is important for the transmission of desired genetic traits. However, effective transmission of these traits depends on many factors including male mating ability, sex-drive and semen quality. Assessment systems attempt to reduce the risk of poor male reproductive performance, while maintaining genetic progress. Such systems commonly involve physical, genital and semen examinations. This review describes the historical development of assessment systems, particularly for bulls, their application and potential areas for future development as influenced by continuing improvements in both knowledge and technology.

Keywords: breeding soundness, libido, male selection.

Resumo

A seleção apropriada do macho bovino para a reprodução é importante para a transmissão dos traços genéticos desejados. Porém, a transmissão eficiente destes traços depende de muitos fatores, incluíndo a habilidade de cópula do macho, libido e qualidade do sêmen. Sistemas de avaliação tentam reduzir o risco de baixo desempenho do reprodutor, enquanto mantendo o progresso genético. Tais sistemas comumente envolvem exames físicos, genitais e de sêmen. Esta revisão descreve o desenvolvimento histórico de sistemas de avaliação, particularmente para touros, sua aplicação e áreas potenciais para desenvolvimento futuro conforme influenciado por melhorias constantes no conhecimento e biotecnias ligadas à reprodução bovina.

Palavras-chave: *estabilidade de reprodução, libido, seleção do macho.*

Introduction

Reproduction in livestock, whether natural or assisted, is an essential pre-requisite for production. The predominant livestock reproductive management system throughout the world remains natural breeding, where a number of factors can influence herd or flock fertility. Some of these factors are male related, some female and others managerial and/or environmental. We currently understand some of these factors and their interactions, whereas others are either unrecognized or poorly understood. However, although there are still many gaps in our understanding, there will always be a strong incentive to solve the remaining questions because of the strong linkage between reproductive performance and the economic viability of livestock enterprises.

In livestock breeding programs, we need to consider the breeding and social contexts in which the male(s) are used; for example whether single or multi-sire breeding is employed (Farin et al., 1982; Godfrey and Lunstra, 1989) and what breeding "pressure" (i.e. ratio of males to cyclic females) is applied (Rupp et al., 1977). An additional consideration is that fertility is usually time sensitive, with penalties being associated with delayed breeding.

Such considerations contribute to a lack of consensus on the relative contributions of a number of different factors to male fertility with the result that we still do not have a single test that reliably predicts fertility of male livestock; a situation that is unlikely to change, despite burgeoning knowledge and emerging technologies.

Historical

The wealth of collective knowledge concerning male reproductive physiology, pathology and behavior that we enjoy today reflects a long and proud history of fruitful inquiry, some of which is relevant to the current discussion. The origins of systematic bull fertility studies may be traced back to work by Williams at Cornell University in the early part of the 20th century and the Swedish program of Lagerlof and Bane. Important milestones included: (1) the rapid development of cattle artificial insemination (AI) following the first successful freezing of bovine semen, (2) the inaugural International Congress on Animal Reproduction and AI (Milan,

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1948) and (3) the initiation of the first ambulatory bull testing program in Colorado (1954). In turn, this last development could not have occurred without technical advances in bull electro-ejaculation (EE) which permitted safe, relatively effective, on-farm semen collection of unhandled bulls. A landmark publication describing the results of 10,940 bull evaluations (Carroll et al., 1963) demonstrated that large-scale bull testing on farm or ranch was feasible. During this period, bull assessment was also gaining ground in South American countries where invaluable experience was being obtained with large herds of Zebu infusion in tropical and sub-tropical environments.

Also at this time, a group of veterinarians in the U.S.A. established the Rocky Mountain Society for the Study of Breeding Soundness in Bulls ''to share and disseminate the essentials for evaluation of beef bulls for fertility and to standardize procedures''. In 1974, this became the American Society for Theriogenology (SFT); an organization which has consistently promoted standardized procedures and standards for bull breeding soundness evaluation (Chenoweth et al., 2010). Standards for bull evaluation have also been published separately in countries such as Australia and Canada. Today, variants of the BSE are used throughout the world with probably the largest numbers of bulls being tested in countries such as Brazil and Argentina. Despite this, it is considered that acceptance of the BSE can be improved in most countries, to the advantage of their respective cattle industries.

The Breeding Soundness Evaluation (BSE)

The breeding soundness evaluation represents a relatively rapid and economic screening procedure for males prior to purchase and/or use for breeding (Chenoweth, 2000). It can also be used retrospectively to diagnose problems. BSE outcomes and components are consistently linked favorably with fertility measures (Chenoweth, 2000; Fitzpatrick et al., 2002). The major elements of the BSE are usually;

1. Physical examination
2. Reproductive evaluation (including measurement of testicular or scrotal size)
3. Semen collection and evaluation, and
4. Report

Other tests may be added, such as those for male libido/serving ability, or to detect reproductive pathogens such as *Tritrichomonas fetus* in bulls.

Genetic considerations

Genetic considerations exist for both favorable and unfavorable reproductive traits. Today there is a long and growing list of inherited faults which can adversely affect male reproduction. These faults include physical problems, such as those involving the genital or locomotory systems. The relatively high heritability of a number of such physical problems in bulls (McNitt, 1965) emphasizes the importance of selecting males which have good structural and genital conformation.

As sires contribute nearly 90% of genetic change in a herd or flock, it is useful to identify male traits which can improve both male and female reproductive efficiency. Bull scrotal circumference is one such trait. It is moderately to highly heritable in beef bulls (approximately 50%) and favorably related to sperm production and semen quality (Brinks, 1994). In addition, a strong genetic links have been established between scrotal circumference in young bulls and age at puberty in related females (Brinks et al., 1978), and other favorable links occur between male and female fertility traits (Perry et al., 1990b). Bull scrotal circumference is an accurate predictor of bull puberty, with remarkable agreement between breeds in pubertal scrotal circumference. Thus, use of scrotal circumference as a selection criterion can improve both immediate and future herd fertility.

However, other less direct genetic considerations are also important in the reproductive selection of males. For example, good male physical conformation and soundness are essential in most livestock breeding systems where male(s) are expected to breed multiple females, each a number of times (Chenoweth, 1997) and within a restricted period in which significant male attrition can occur (Ellis et al., 2005). Further emphasis on the importance of good male structural soundness comes from a growing list of genetic physical and seminal faults which can adversely impact male reproduction.

Finally, genetic considerations should include the relationships between and among production and reproduction traits (Ologun et al., 1981; Vargas et al., 1998) well as their environmental interactions. These will become more important in male reproductive selection as genetic databases and selection tools become more refined and accurate.

Sperm abnormalities

Sperm structure is, in general, related to function, with "abnormal" sperm being implicated in failure of both fertilization and pregnancy outcomes. Sperm abnormalities have been associated with male infertility and sterility in most species studied. The causes of defective sperm structure may be environmental, genetic, or a combination of both, with environmental causes considered most common. These abnormalities vary from morphological defects evident upon clinical examination, to those which are more subtle.

Biomarkers for sperm damage

Damage to the spermatogenic epithelium, as well as to developed sperm, represents the outcome of a limited number of pathogenic pathways or mechanisms. This is useful in our search for biomarkers for such damage. With common underlying mechanisms at work, it would not be unexpected to find a number of sperm abnormalities occurring consistently, either concurrently or in series, in response to a variety of stressors. One example of a consistent pattern of sperm morphological abnormalities occurs with the diadem/crater defect, which represents part of a stereotyped temporal spermatogenic response to a wide variety of stressors (Larsen and Chenoweth, 1990). This response has been characterized in different species using a testicular insulation model (Vogler et al., 1993) whereby a consistent temporal series of abnormalities is associated with the duration and severity of stress. Sperm containing diadem/crater defects have been shown to result in lowered embryo quality and survivability (Saacke et al., 1992); even those sperm containing subtle (i.e. non head-distorting) forms of this defect are able to access the ovum, leading to both lowered fertility and decreased embryo quality (Miller et al., 1982; Saacke et al., 1992).

In addition to the diadem/crater defect, a number of other "bio-markers" for sperm damage have been identified using tools such as proteomics, fluorescent probes and high-definition microscopy, including differential interference phase contrast (DIC). The latter has advantages as a routine diagnostic tool because it can be used to detect damage to a number of essential sperm functions, such as those associated with the nucleus, acrosome, principal piece and membranes.

Compensable and uncompensable semen traits

Abnormal sperm may reduce fertility in one of two ways: (1) failure to reach the fertilization site; or (2) either inability to either fertilize the ovum or to sustain development of the early embryo. In the first case, failure of sperm to reach the fertilization site can often be traced to problems in sperm transport. Those defects which cause either impaired sperm motility, or reduced probability of successfully transcending the female tract, are termed compensable defects. This is because a theoretical increase in numbers of functionally competent sperm will compensate for those that are unable to the journey. Those defects which lead to failed fertilization or early pregnancy loss are termed uncompensable (Saacke et al., 2000). With such defects, an increase in sperm numbers alone will theoretically not advantage fertility.

Genetic sperm defects

Genetic sperm defects are those which have been shown to have a genetic mode of transmission (Chenoweth, 2005). A number of sperm defects in different species may be categorized as genetic in origin with this number increasing as diagnostic capabilities improve. The knobbed acrosomes (KA) defect is one example, and which can be either genetic or environmental in origin. Sperm containing KA either lack the ability to attach to ova (Buttle and Hancock, 1963) or have reduced capability to do so (Thundathil et al., 2000). In addition, apparently normal sperm obtained from animals affected by KA may also be compromised (Thundathil et al., 2000), as represented by damage to membranes or chromatin, premature capacitation and spontaneous acrosome reaction (Thundathil et al., 2002).

Abnormal sperm thresholds

Early researchers were convinced that there was a "threshold" of observable sperm morphological abnormalities for a given bull, above which fertility became compromised. For example, Lagerlof (1936) stated "if pathological spermatozoa constituted more than 20% of a given sample, then the bull may be of reduced fertility". In turn, he cited Williams and Savage (1927), viz; "no highly efficient bull emitted more than 170 abnormal sperms per thousand". Herman and Swanson (1941) stated that "bulls which produced semen containing over 30 per cent of abnormal spermatozoa were usually of poor fertility". These observations were based upon work with A.I. bulls, which could normally be expected to have superior fertility traits. However, Wiltbank and Parrish (1986), working with naturally mated cattle in Texas, found that bulls pre-selected for good sperm morphology (≥70 or 80% normal) achieved significantly more pregnancies than unselected bulls, and that 70% normal sperm represented a logical threshold for "normal" sperm.

Support for the "threshold" concept also comes from less likely sources. For example, Amann et al. (2000), using IVF, found that bull semen containing >30% proximal droplets and <25% other abnormalities had severely compromised fertility as measured by fertilization and cleavage rates. Other IVF work, including human, has reinforced this "threshold" including that of Evenson et al. (1999), working with both IVF and IUI, who conclude that “the probability of fertilization seems to be close to zero if the proportion of cells with DNA damage (as detected by CASA) exceeds 30%”. Although the mechanisms at work here are not fully understood, it is possible that damaged sperm adversely affect their immediate environment, and above a critical number or mass, this can affect the general sperm population.

Male libido/Sex drive

Libido, or sex-drive, in male livestock, a measurable trait (Blockey, 1978; Chenoweth et al., 1979) represents an important component of male fertility (Chenoweth, 1981) and one with a strong genetic component (Chenoweth and Landaeta-Hernandez, 1998). Using bulls of higher sex-drive has been reported to benefit pregnancy rates, time of conception, length of calving season, homogeneity of weaned calves and more efficient use of labor (Blockey, 1978, 1989; Godfrey and Lunstra, 1989).

However, other studies have shown poor or inconclusive relationships between bull libido/serving capacity assessments and herd fertility. In some studies, although higher libido bulls serviced more often, and serviced more females, than lower libido bulls, more pregnancies did not result.

Some factors may contribute to these mixed findings, including the inherent difficulties of demonstrating single male trait effects on herd or flock fertility. This last concern is important as male libido is just one of a number of factors which influence herd or flock fertility; BSE components (scrotal circumference, sperm motility and morphology) separately influence fertility and do not appear to be genetically linked with behavioral traits such as libido. Thus, although bulls may be superior in one or more traits, their fertility can be compromised by deficiencies in others. This was well illustrated in one study using bulls with synchronized heifer (Farin et al., 1989) in which differences in bull libido (and sexual activity) were confounded by differences in breeding soundness traits.

The consensus from a number of studies thus appears to be that libido and serving capacity tests are useful in differentiating bulls on the basis of breeding (or mating) activity, as well as in qualitatively assessing mating ability. However, the results of such tests do not necessarily predict fertility.

Composite bull assessment schemes

A number of factors influence herd fertility, and these do not always work in harmony. These can include bull BSE values as well as behavioral factors such as the expression of libido and social rank. Attempts have been made to combine a number of these factors to best predict bull fertility. For example, in one study (Holroyd et al., 2002), a regression model was used to predict bull fertility in multi-sire breeding where paternity was determined by blood typing. The most important traits were found to be scrotal circumference, back-fat, sperm morphology (particularly primary abnormalities) and libido. This model accounted for 37% of the variance in fertility of yearling bulls and 22% for 2 yr-old bulls. This was consistent with another study (Perry et al., 1990a) in which similar measures were shown to influence bull fertility. Here, best relationships with bull fertility in single-sire herds involved multiple traits including semen quality, sex-drive and social status, emphasizing that most accurate male reproductive selection relies on a number of measured traits.

Conclusions

We are fortunate today in witnessing renewed interest in many aspects of male livestock reproduction; an area of inquiry relatively neglected for much of the modern era. This is represented by increasing numbers of relevant publications and presentations as well as by the formation of new groups such as the Association for Applied Animal Andrology (www.animalandrology.org). Much of this activity is driven by powerful new technologies involving a number of different disciplines. It has also been accompanied by increased interest in animal behavior and recognition of its importance in relation to good reproductive selection and management.

However, it is important for practical applications (including appropriate education and training) to keep pace with these rapid developments, many of which are in areas of basic research. Today, there is an even greater need than ever to integrate and apply such new knowledge to livestock systems. The challenge is to bring these threads from different worlds together for the practical benefit of the livestock industries.

Some recent areas of inquiry may help in this regard. For example, linked marker/quantitative trait loci can be used to accurately establish paternity in multi-sire herds (Holroyd et al., 2002). This provides a powerful tool for establishing not only the reproductive performance of individual bulls, but also important genetic information via their offspring. Unfortunately, such information, although unique and highly valuable, is retrospective. For most predictive reproductive selection, the use of multiple traits as a male fertility ‘‘index” holds promise. This, however, begs the question of which traits to include in such an index; an area of great potential for fruitful investigation, especially with the benefit of the knowledge and technology available today.

Male breeding soundness evaluation, while being constantly refined, has proven to be a cost-effective procedure throughout much of the world. Timely, effective sire evaluation provides many benefits including risk-reduction, efficient sire-usage, improved herd/flock fertility, and genetic benefits for both male and female offspring.

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