

Assessment of the boar reproductive efficiency: physiology and implications

Avaliação da eficiência reprodutiva do varrão: fisiologia e implicações

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Abstract

The main objective of a boar stud is to produce a large volume of high-quality semen per boar in an efficient and safe manner. This includes: the management of the anatomy, physiology and sexual behaviour of the young boar, that influences its performance as an adult. Normal reproductive activity in boars is coordinated by the endocrine and nervous system. Abnormal activity in one or more of these areas can result in reproductive problems. For the development of the sexual behaviour is important to considerer plays and social conditions of rearing of penmates. Play in animals is common in mammals, frequent in young and is not oriented to satisfy the immediate needs and carries appreciable costs in energy, time and even physical risk. Although, play contributes to the development of several functions that take place in the adult. Sexual behavior begin as early as 1 month of age in boars; mounting activity of penmates is observed more frequently for males than females. Some authors emphasized the importance of social conditions during rearing, due to the sexual activity showed in pubertal boars.

Keywords: boars, reproduction physiology, sexual behaviour.

Palavras-chave: varrão, fisiologia reprodutiva, comportamento sexual.

Introduction

The increased use of AI has dramatically increased the number of boars needed for semen collection on a daily basis. The main objective of a boar stud is to produce a large volume of high-quality semen per boar in an efficient and safe manner.

The boar: anatomy and sexual behaviour

Anatomy of the boar

The male reproductive system is composed of a variety of different structures including the testes; the urogenital duct system; the secondary sex glands; the pituitary gland; and the hypothalamus. These communicate via the endocrine and nervous system to coordinate normal reproductive activity in boars. Abnormal activity in one or more of these areas can result in reproductive problems.

The testes are majority formed by seminiferous tubules. The seminiferous tubules are a convoluted network of ducts in which spermatozoa are produced. Sertoli cells are specialized cells involved in the maturation of spermatozoa and hormone production. Interstitial cells of Leydig, blood and lymph vessels and nerves are located in between the seminiferous tubules. Important interactions between the Sertoli and Leydig cells regulate virtually every aspect of male reproductive function.

The external location of testis needs an anatomical system for thermoregulation, formed by a complex vascular arrangement of testicular arteries and veins in the spermatic cord called the pampiniform plexus (Garner and Hafez, 1993). The testicular artery forms a convoluted structure in the shape of a cone in which arterial coils are enmeshed with testicular veins. From a functional perspective, this countercurrent mechanism enables arterial blood entering the testis to be cooled by venous blood exiting the testis. In most species, the temperature of arterial blood drops between 2 and 4°C prior to its entry into the testes.

Two groups of muscles, the tunica dartos and cremaster, play an important role in thermoregulation. The tunica dartos lines the inside of the scrotum and controls its proximity to the testis. It contracts during cold weather pulling the scrotal sac closer to the testis for added insulation and relaxes during warm weather allowing the scrotum to recoil into a distal position. The cremaster muscle is located in the spermatic cord and is attached to the thick membranous sac surrounding the testis. It contracts during cold weather pulling the scrotal sac and testis closer to the body core and relaxes during warm conditions allowing the testis to return to its normal position. Both muscles have an abundant supply of nerve fibers that respond to temperature sensors located in the central nervous system. Because boars do not have pendulous testicles like bulls, the tunica dartos is more important than the cremaster muscle in the regulation of testicular temperature.

The epididymis forms three distinct sections - the caput (head), corpus (body) and cauda (tail)

epididymi. The convoluted duct of the epididymis is surrounded by a prominent layer of circular muscle fibers and contains pseudostratified columnar, stereociliated epithelium.

Spermatozoa become motile and acquire fertilizational competence in the body of the epididymi due to the secretion of factors by the cells located in this region. Movement of spermatozoa through the epididymi is thought to be due to the flow of rete fluid, the action of the stereociliated epithelium and contractions of the circular muscle layer. Unejaculated spermatozoa are gradually eliminated by excretion into the urine. Spermatozoa that are not excreted in the urine undergo a gradual aging process. During the aging process, fertilizational competence is lost first and is followed by a decrease in motility (Garner and Hafez, 1993). Eventually, dying spermatozoa disintegrate. Ejaculates with dying spermatozoa often appear "clumpy", ie. - have large groups of spermatozoa bound together by their heads.

The vas deferens is a thick, heavily muscled tube through which sperm are transported from the tail of the epididymis to the pelvic urethra, at which point the paired genital systems of the boar meet and converge with the urinary tract just before the bladder. Adjacent to the pelvic urethra are three secondary sex glands: the vesicular glands or seminal vesicles; the prostate gland; and the bulbo-urethral glands.

The seminal vesicles lie lateral to the terminal portion of each vas deferens. In the boar, they are large, lobulated and relatively diffuse. They often appear to have an orange color. They are responsible for the majority of the fluid volume of boar semen. In addition, they secrete high levels of fructose and citric acid as well as inositol, ergothioneine, several amino acids and glycerylphosphoroylcholine. Most of these compounds are used as energy substrates by ejaculated spermatozoa (Garner and Hafez, 1993).

The prostate gland is located next to the vesicular glands with the majority of its body being embedded in the muscle layer surrounding the pelvic urethra. Secretions from the prostate gland during ejaculation are primarily alkaline and contain calcium, acid phosphatase and fibrinolysin. The primary function of the fluid from the prostate gland is to neutralize the acidic vaginal secretions. Secretions from the prostate gland also are believed to give semen its characteristic odor.

The bulbourethral glands are long cylindrical glands in the boar located on either side of the pelvic urethra near the ischial arch of the pelvis. The bulbourethral glands secrete the gel fraction of the semen characteristic of porcine ejaculates. Many functions for the gel component of semen have been postulated, but few have been proven.

The terminal portion of the boar's urogenital system is the penile urethra, which is the central tube within the penis. The penile urethra opens into the glans penis. In the boar, the glans penis has a counter clockwise spiral. The glans penis is highly innervated and must be stimulated properly for normal ejaculation to occur.

In young prepubertal boars, the glans penis cannot be extended fully because it is fused with the lining of the prepuce. As a boar matures, androgen produced by the testis initiate keratinization of the inner preputial lining and the penis is eventually freed from its connection with prepuce. Persistent frenulum is a condition in which strands of tissue did not keratinize fully and are still attached to the penis (Garner and Hafez, 1993). When this occurs, the end of the penis curves back toward to the prepuce during erection and ejaculation. Removal of these strands of tissue with a pair of sterile scissors corrects this situation. Contents of the preputial sac are often expelled during detection of estrus or natural matings and often believed to be the source of the odor associated with mature boars.

Physiology of the boar

In the boar, high quantities of estrogen are found in semen. The source of these estrogens is the sertoli cells, which convert testosterone to estrogen via the aromatase enzyme (Setchell *et al.*, 1993).

It appears that the primary role of seminal estrogens is to stimulate important reproductive events in the female reproductive tract during breeding.

Spermatogenesis

Spermatogenesis is divided into two basic processes: spermatocytogenesis and spermiogenesis. In a general sense, spermatocytogenesis is the process involved with the mitotic and meiotic divisions of sperm cells, while spermiogenesis refers to the maturational phase of development. Although both hormones are important, it is believed that LH plays a more active role than FSH in spermatocytogenesis, while FSH is the main hormone involved with spermiogenesis.

Spermatocytogenesis

Just prior to puberty in boars, undifferentiated germ cells called gonocytes differentiate to form type AO spermatogonia. These are the precursor sperm cells from which all other sperm cells originate. There is some evidence that the number of AO spermatogonia is directly related to the sperm production capacity of adult males. In adult boars, AO spermatogonia differentiate into A1 spermatogonia which divide progressively to form various types of immature sperm cells. The final mitotic division during spermatocytogenesis occurs in primary spermatocytes.

Although the average number of mitotic divisions cells would undergo between the A1 and primary spermatocyte stages is a subject of some controversy, a figure of 6 to 8 is commonly used (Garner and Hafez, 1993). This means that between 32 and 124 primary spermatocytes are formed from single spermatogonia.

Spermiogenesis and Spermiation

The round spermatids are transformed into spermatozoa by a series of morphological changes referred to as spermiogenesis. Maturation changes that spermatozoa undergo during spermiogenesis include condensation of nuclear material, formation of the sperm tail and development of the acrosomal cap and its contents (Garner and Hafez, 1993). During most of spermiogenesis the sperm cells appear to have their heads imbedded in Sertoli cells. In reality, the membrane of the Sertoli cell actually is wrapped around the sperm head. Communication and exchange of materials between the Sertoli and developing sperm cells occurs via intercellular bridges. The actual release of spermatozoa into the lumen of the seminiferous tubule is called spermiation. The elongated spermatids are gradually extruded or pushed out of the Sertoli cell into the lumen of the seminiferous tubule until only a small cytoplasmic stalk connects the head of the sperm to the residual body in the Sertoli cell. Breakage of the stalk results in the formation of a cytoplasmic droplet in the neck region of the sperm. These commonly are referred to as proximal cytoplasmic droplets.

Epididymal maturation

Spermatozoa enter the head of the epididymis incapable of fertilization; however, acquire this ability at some point during their transit to the cauda epididymis. It is believed that epididymal secretions contain maturation factors that stimulate biochemical changes within the sperm cells necessary for fertilization (Garner and Hafez, 1993; Setchell *et al.*, 1993). These changes include development of the potential for progressive forward motility; alteration of metabolic mechanisms; loss of the cytoplasmic droplet; and changes in the plasma membrane, acrosomal cap and nuclear material.

The entire process of spermatogenesis requires 45 to 55 days in the boar. The majority of this time is spent in the testicle and involves changes associated with both spermatocytogenesis and spermiogenesis. Maturation in the epididymis is thought to require only 10 to 14 days.

Sexual behaviour

Certain aspects of sexual behavior begin as early as 1 month of age in boars. Mounting activity of penmates is observed more frequently for males than females. Consistent mounting activity accompanied by erection occurs around 4 months of age. However, most boars are not capable of producing ejaculates with normal quantities of fertile spermatozoa until 6 to 8 months of age. In general, testosterone is the male hormone that is the most closely linked with sex drive or libido. It is true that castrated males or boars with extremely low testosterone levels exhibit virtually no sexual interest. However, there have been a number of documented cases in which boars with normal levels of testosterone have low libido. Consequently, determining the relative importance of the endocrine system and prior sexual experience in male reproductive behavior is extremely difficult.

Development of sexual behaviour

Play in animals is common in mammals, frequent in young and is not oriented to satisfy the immediate needs and carries appreciable costs in energy, time and even physical risk. Although, play contributes to the development of several functions that take place in the adult (Dobao *et al.*, 1984) There is a behavioral dimorphism of plays in mammals, and there is a higher play activity in males than in females. Hemsworth *et al.* (1977) emphasized the importance of social conditions during rearing, due to the more sexual activity showed in pubertal boars reared without social restrictions than those maintained in isolation.

Sex plays are common between piglets and might be related with the sexualization process. They appear few weeks after birth and reach a peak during the second neonatal month. These plays are similar of the sexual behavior of puberty adults. The sex play of male piglets is characterized by the pattern of behavior of the adult boar: sniffing the genital region and mounting accompanied by pelvic movements, meanwhile females present a characteristic receptive sexual reaction (Berry and Signoret, 1984)

The sexual differentiation process varies in magnitude between species. Sexual differentiation of reproductive function in domestic pigs is a unique model in comparative biology because differentiation of sexual behavior occurs post-natal during pubertal development (Ford, 1990). The defeminization is the suppression in males of the capacity to display female behavior. Defeminization is a post-natal process in species with a short period of gestation (hamster, mice and rats) and in species with a long period of gestation, occurs either pre (guinea pigs and sheep) or during farrowing (dogs). Based on length of gestation, the sensitive period for suppression of female behavior in male pigs would likely occur prenatal, although it was suggested that the sensitive period for sexual differentiation in male pigs is associated with increased testosterone secretion during

pubertal development (Ford, 1982), that has a progressive increase during prepubertal period. In male pigs, increases in testosterone secretion are evident in three stages of development: day 35 as a fetal, the first three weeks of life and after 4.5 months of age (Ford, 1982)

All this mentioned above, contributes to determine that the best period to study the sexualization of young pigs is the lactation period, due to the increase in the secretion of steroid hormones and due to the playing activity that piglets develop during this period.

The spermatozoa: morphology and physiology

The observation of the spermatozoa by van Leeuwenhoek some 300 years ago gave rise to certain fantasies as to the nature of their function, for instance, the oft-quoted concept of the homunculus of Hartsoecker.

The spermatozoon is the most dramatic example at the cellular level of the potential for evolutionary adaptation to functional needs. It is a high polarized economical cell formed by an assembly of distinctive organelles essentially all of which contribute directly to its specialized role.

The appearances of the acrosome in the light microscope produce some confusion in the past as to the structure involved, and consequently some difficulty with terminology. Ultrastructural studies now make it clear that the acrosome is a membrane limited vesicle applied over a variable portion of the rostral surface of the sperm head in the form of a cap. Questions have been raised also to the homology of the acrosome content with that of lysosomes present in other cell types. The enzymes believed to be present in the acrosome are: hyaluronidase, proacrosin, acrosin, cathepsin D, dipeptidyl peptidase II, esterases, neuraminidase, acid phosphatase, phospholipase A, phospholipase C, arylsulphatase, β -N-acetylglucosaminidase, acid proteinases, collagenase.

A unique feature of eutherian spermatozoa is a stable defined posterior segment of the acrosome. This was first called the "equatorial segment" because of its central moon-shaped position in spade-shaped spermatozoa such as those of the bull and rabbit. The equatorial region is characterized by an absolutely parallel arrangement of the outer and inner membranes of the acrosome. Anterior to the equatorial region, the outer and inner membranes of the acrosome have a conventional trilaminar appearance in thin sections, but display an asymmetry of the inner and outer leaflets of the bilayer.

In the fertilizing spermatozoon, enzymes are released as a result of the acrosome reaction. This reaction is an essential preliminary to the fertilization. It appears to be heralded by an increase of the intra-acrosomal pH of about one pH unit (the compartment of the acrosome is apparently maintained at a pH below 5.0) and certainly involves point fusions of outer acrosomal membrane with the plasma membrane overlying it; thus creating pores through which the enzymatic content may escape. The initial fusion reaction appears to take place at the anterior border of the equatorial segment rather than at the apex of the acrosome.

A few studies suggest a role at some points for certain acrosomal enzymes in development of the reaction. This is accompanied by auto-catalytic activation of pro-acrosin to acrosin and its release, probably in concert with hyaluronidase and other acrosomal hydrolases.

The **nucleus** of the mature spermatozoon is characterized generally by highly condensed chromatin and has a species-specific shape determined by the genetic constitution of the germ cell itself. The chromatin is composed primarily of DNA closely complexed with cysteine-rich protamine. Flow cytometry methods confirm that X-bearing spermatozoa contain 3.5-4.5% more DNA than Y-bearing spermatozoa. It is certain that sperm DNA is inactive and does not replicate until protamines are displaced in the hours that follow sperm entry into the egg.

A conventional sperm **tail** generates the propulsive force, considered essential for penetration of the egg investment. There is a prominent connecting piece that links the tail with the head, 9 outer dense fibres around the axoneme, mitochondria outside the dense fibres arranged anteriorly as a sheath, and a fibrous sheath that covers the principal piece of the tail. The kinetic apparatus of the sperm tail is the axoneme or axial filament complex. The axoneme consists of 9 microtubule doublets arranged in a circle around a central pair of single microtubules.

The metabolic properties of the mammalian spermatozoa resemble those found in somatic cells. The primary interest, finally, lies in metabolic events in the tail compartment that allow spermatozoa to elaborate ATP, and how that is utilized to produce the energy required for flagellation. Mammalian spermatozoa respire, glycolyze and degrade lipids by enzymatic mechanisms basically similar to those in other cells. The spermatozoa have the ability to produce ATP through glycolytic degradation of simple sugars such as glucose, fructose and mannose; more complex carbohydrates (e.g. sucrose) cannot be used.

The potential of active-gaining movement is not displayed by spermatozoa released from the testis, this develops only as they move through the epididymis. Mature spermatozoa stored in the epididymis are immotile or nearly so. Active motility develops only at ejaculation, often instantly, as a result of the neutralization of suppressive factors.

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