Anatomy and Physiology of the Stallion

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INTRODUCTION

The financial commitment associated with breeding horses can be considerable. Most small breeding operations are economically centered around one or two stallions. Problems which compromise a stallion's fertility essentially affect all mares which are not in foal. Thus, the ability of a stallion to produce adequate, fertile spermatozoa is essential for an economically successful breeding season.

Current equine foaling rates are between 55 and 60 percent. Obviously, there is considerable room for improvement in reproductive efficiency. Reproductive efficiency can be improved through a better understanding of the stallion's anatomy, physiology and behavior. This understanding will allow for the detection and management of changes which influence the stallion's ability to produce spermatozoa. Detection early in the breeding season will allow management to make decisions that may avoid costly delays associated with a group of open mares. The following sections review the reproductive anatomy and physiology of the stallion as related to everyday breeding management.

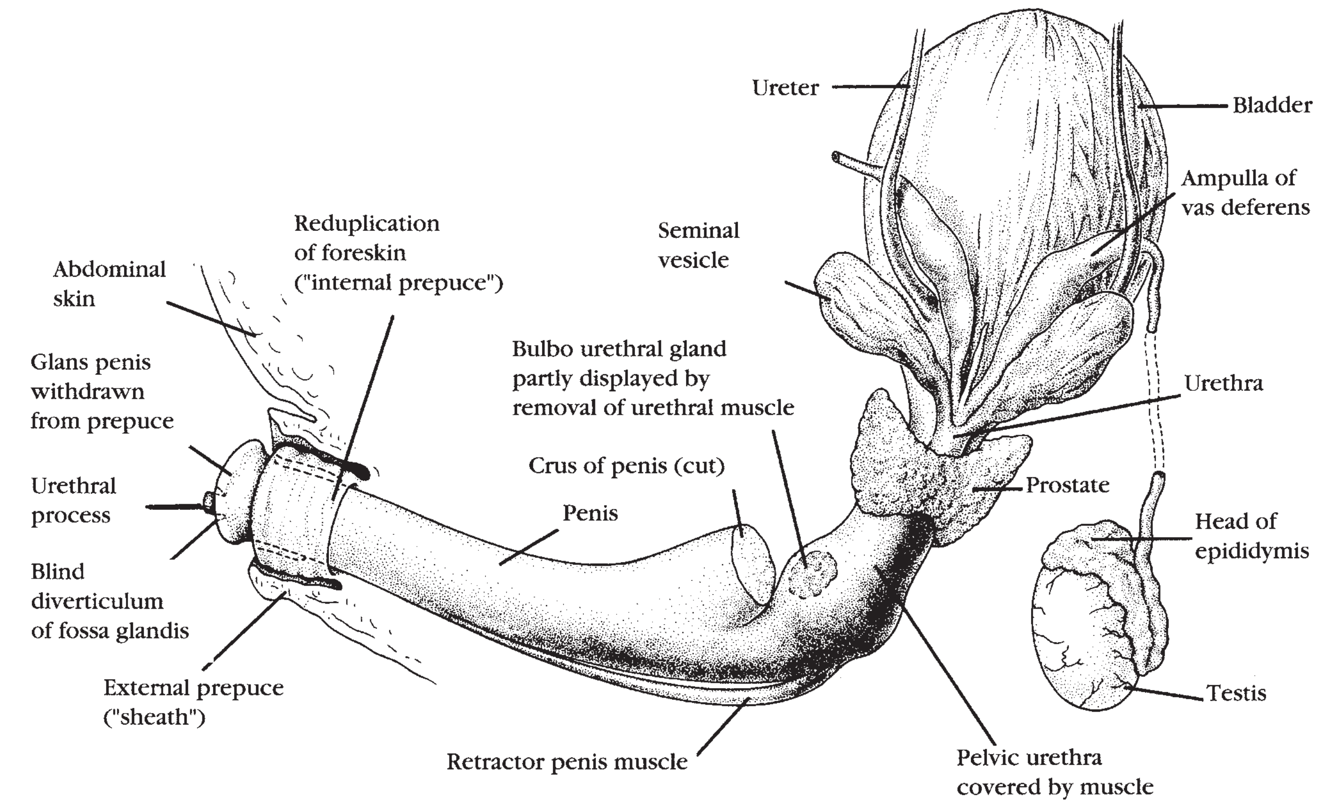

Figure 1: **Reproductive tract of the stallion (lateral view).** Bladder and upper urethra are twisted to expose posterior aspects. (From Eckstein and Zucherman, 1956.)

ANATOMY

The stallion's reproductive system (Figure 1) includes two testes with attached epididymides, two deferent ducts, urethra, penis and accessory sex glands (bulbourethral, prostate and vesicular).

The testes can be considered the 'master organ' of the male's reproductive system because the testes are the site for production of spermatozoa (spermatogenesis) and the primary male sex hormone, testosterone. The stallion's testes are normally ovoid in shape, measure 80 to 140 mm long and 50 to 80mm wide, and weigh approximately 225 grams. Testicular size should be evaluated during reproductive/prepurchase exams, as testicular size is related to the stallion's ability to produce spermatozoa. Generally, as testicular size increases, the potential ability to produce spermatozoa increases.

In addition to individual differences in testicular size, seasonal and age variations exist as well. During periods of short daylight length, when testosterone concentrations are depressed, testicular size is smaller as compared to testicular size during the normal breeding season when daylight periods are long and testosterone concentrations highest. The small testicular size during the winter months corresponds to decreased sperm production and may necessitate stricter management of some stallions, depending on the number of mares booked, and the stallion's ability to produce spermatozoa. In some species, maximum testicular size is achieved shortly after puberty: however, testicular size increases in the stallion until much later in life (12-13 years).

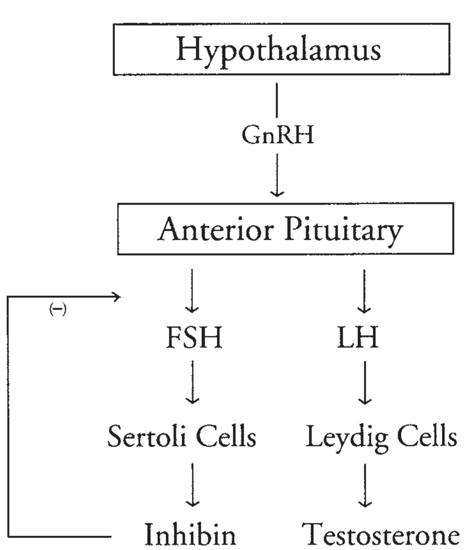

Figure 2: Hormonal control of reproductive function in stallion—simplified diagram. GnRH—gonadotropin releasing hormone, LH—luteinizing hormone and FSH—follicle stimulating hormone.

Normally, stallions have two testicles descended in the scrotum. The retention of one (unilateral) or both (bilateral) testicles in the body cavity occurs fairly frequently in stallions and is referred to as cryptorchidism. Unilateral cryptorchids are generally fertile, although sperm production is generally lower than the average sperm production of stallions with two scrotal testes. Bilateral cryptorchids will display normal secondary sex characteristics, but are infertile due to suppressed spermatogenesis. Although the exact cause of cryptorchidism is unclear, it is currently thought to be an inheritable trait, and some breed associations prohibit the showing and/or breeding of cryptorchid stallions.

HORMONAL CONTROL

Hormonal control of reproductive function involves a center in the brain known as the hypothalamus, a small gland located at the base of the brain known as the pituitary gland, and the testes. A simplified scheme (Figure 2) involves the release of gonadotropin releasing hormone (GnRH) from the hypothalamus, which travels through portal blood vessels to the anterior pituitary. At the anterior pituitary, GnRH stimulates the secretion of the gonadotropins, follicle stimulating hormone (FSH) and luteinizing hormone (LH). These gonadotropins travel to the testes, where FSH exerts its effect on the Sertoli cells and LH on the Leydig cells.

Sertoli cells are located within the testes' seminiferous epithelium and function primarily in supporting spermatozoa development. Sertoli cells also secrete a number of proteins which function in the regulation of FSH release from the anterior pituitary gland, and proteins which bind testosterone. Leydig cells are located between the seminiferous tubules, and under the influence of LH, are responsible for testosterone production. In addition, Leydig cells secrete estrogens. Although stallions are known to produce high concentrations of estrogen, the exact physiological function of estrogen is unclear.

As previously mentioned, testosterone is necessary for normal sexual behavior and testicular function. In fact, testicular concentrations of testosterone are considerably higher than systemic concentrations, and are necessary for proper testicular function. The proteins produced by Sertoli cells which bind testosterone are responsible for maintaining the necessary testicular concentrations. Testosterone concentrations control the release of GnRH and the gonadotropins (and thus its own concentration) through a negative feedback system. When concentrations of testosterone are 'high,' the system slows down testosterone production due to the inhibition of the hypothalamus and anterior pituitary gland. Likewise, when testosterone concentrations are 'low,' there is no inhibition and the system increases testosterone production.

When anabolic steroids are administered to stallions, the system recognizes the exogenous hormone as testosterone, and thus, hypothalamic and anterior pituitary activity is inhibited. Testosterone concentrations are actually reduced when animals are receiving anabolic steroids. Therefore, the stallion displays normal sexual behavior, but testicular size and sperm production are severely impaired. Sperm production will remain reduced for as long as the exogenous hormone is being administered and will not return to a normal level of production for approximately two months after cessation of treatment.

Hormonal control is under seasonal modification. When daylight periods are short, a gland located within the brain known as the pineal gland releases melatonin. Melatonin is thought to inhibit the hypothalamus from releasing GnRH, which subsequently decreases LH and testosterone production. Thus, during periods of short daylight (winter), male reproductive function is suppressed due to low testosterone concentrations. During this time testicular size and sperm production are reduced, and although sexual behavior is variable, it is not uncommon for stallions to have low sexual drive (libido), and to require a longer time to mount and ejaculate.

Stallions can be placed under artificial light to increase testicular activity. This may be advantageous for stallions breeding a larger book of mares early in the winter and who have low libido and/or daily sperm production during the winter months. Stallions will require photostimulation similar to that used to increase reproductive cyclicity in mares. Normally, stallions are exposed to a total day length of 16 hours beginning in December. Testicular size and sperm production will approach 'normal' breeding season values in approximately 60 days. Stallion managers must recognize that stallions must be exposed to a period of short day length in the fall, otherwise the stallions will not respond to photostimulation, and testicular activity (testosterone production and spermatogenesis) will be reduced to nonbreeding season levels. At this time stallions would have to be exposed to short day lengths to re-establish their responsiveness to photostimulation.

SPERM PRODUCTION

Spermatogenesis occurs within the seminiferous epithelium and serves two primary purposes: first, spermatogenesis maintains a population of uncommitted germ cells from which future spermatozoa can be produced. Secondly, spermatogensis results in the formation of committed germ cells (Spermatogonia) which eventually give rise to spermatozoa. This process involves a series of events which can be divided into three phases; spermatocytogenesis, the initial differentiation and subsequent division of spermatogonia to increase their number; meiosis, the process where genetic rearrangement occurs between homologous chromosomes, and where spermatogonia are reduced in chromosome number by division to form spermatids; and spermiogenesis, where spermatids differentiate into mature spermatids. Once spermatids are released from the seminiferous epithelium into the lumen of the seminiferous tubule they are referred to as spermatozoa. Each of these three phases requires 18-19 days, and the entire series of events leading to release of spermatozoa requires 57 days.

Once spermatozoa are released within the seminiferous tubules, they travel through a series of ducts to the epididymis, which is lightly attached to the dorsal surface of the testis. The epididymis can be divided into three segments; the head (caput), body (corpus) and tail (cauda). Within the epididymis, spermatozoa undergo modifications (maturation) in which they acquire the ability to swim and to fertilize an egg. Most of these changes are complete by the time spermatozoa reach the end of the corpus. The migration of spermatozoa through the epididymis requires approximately 8 days. Most of the spermatozoa are stored in the tail of the epididymis until ejaculation. When stallions are not being collected or bred on a frequent basis, spermatozoa are released from the epididymis and voided in urine. The exact length of time in which spermatozoa can be accumulated in the epididymis is unknown, but probably varies among stallions.

The length of time required for spermatogenesis and epididymal maturation is species specific and is approximately 65 days in the stallion. This is a statistic every stallion manager should be familiar with because administration of anabolic steroids, illness (fever), and/or trauma to the testes can lower sperm production, and "normal" production will not be restored for this time period (i.e., 65 days).

DAILY SPERM OUTPUT

The minimum number of spermatozoa produced within a 24-hour time period is known as daily sperm production (DSP). DSP varies among stallions and, as previously mentioned, is influenced by testicular size.

Daily sperm output (DSO) refers to the number of spermatozoa which can be collected per 24-hour period from a stallion and is determined by collecting the stallion daily for 7 days. At this time the extragonadal reserves of spermatozoa, found primarily in the tail of the epididymis, are depleted. The number of spermatozoa in the ejaculate after 7 days of daily collection reflects sperm output since last collection. During the winter months, when testosterone concentrations are low, the number of motile spermatozoa available for insemination is approximately half the number available during the breeding season. This may limit the number of mares which can be bred during the winter months, and will depend on a given stallion's DSO.

It is important that stallion managers recognize that there are only so many spermatozoa available for ejaculation. A common misconception is that frequent semen collections will increase the number of spermatozoa produced. The time required for spermatogenesis and epididymal maturation is independent of ejaculation frequency. If a stallion is collected daily, or even twice daily for several days, the number of spermatozoa present in the ejaculate will represent that stallion's capacity to produce spermatozoa in the last 12 or 24 hours. More importantly, the number of spermatozoa available per week for stallions collected daily or every-other-day, does not differ. The number of sperm present in the ejaculates of stallions collected daily reflect DSO, and the number present in stallions collected every-other-day represent DSO plus extragonadal reserves developed over 24 hours.

In management terms, as long as the stallion's libido (and DSP) is adequate, semen collections daily, or even twice or three times daily (common for operations using live cover) will not interfere with the stallion's ability to produce sperm. Likewise, every-other-day collections in an artificial insemination program will harvest the maximum number of sperm available from a stallion. A stallion's DSP should be determined, as it will allow stallion managers to determine how many potential mares or breedings can be booked during a given time period. In addition, a stallion's DSO should be monitored as changes in DSO may be an indication of testicular changes which could affect future sperm production.

TEMPERATURE CONTROL

The testes are suspended within the scrotum by the spermatic cord and associated cremaster muscle. The scrotum is a somewhat pendulous sac which has a primary function of maintaining proper temperature for sperm production. Muscles associated with the scrotum (tunica dartos) and the spermatic cord (cremaster) contract during cool weather to draw the testes close to the body to raise testicular temperature. Likewise, during high ambient and/or body temperature, the testes are dropped away from the animal's body to aid in lowering testicular temperature. During high ambient temperatures, the scrotum becomes pendulous and increases in surface area. This also aids in temperature control due to the presence of a high number of sweat glands in the scrotal skin. Thus, testicular temperature is partly regulated through evaporation of sweat. In addition to the contractile nature of the scrotum, thermoregulation is achieved by heat transfer between arterial blood entering the testes and venous blood leaving the testes. The network of arteries and veins responsible for this heat exchange is referred to as the pampiniform plexus.

The scrotum's ability to regulate testicular temperature is essential for maximum reproduction efficiency. Trauma to the testes, which results in adhesions or edema, could decrease their ability to respond to temperature changes. Elevated testicular temperatures, even for a short duration (e.g., 37° C for 24 hours), can significantly lower the number as spermatozoa available for fertilization. Because spermtogenesis and epididymal maturation require approximately 65 days, short bouts of elevated testicular temperature will necessitate strict management of a stallion's book for two months.

PENIS

The stallion's penis is classified as a musculocavernous type, and consists of a root, which attaches the penis to the skeleton; the main body (shaft) of the penis; and the glans penis, which is the free end of the penis. In the nonerect state, the stallion's penis is approximately 50 cm in length, 3 to 5 cm in diameter, and is contained within the sheath or prepuce, which forms two folds around the free end of the penis. The first fold forms the preputial orifice, and the second fold forms the preputial ring (Figure 1). Because of the presence of a high number of sebaceous glands, it is common for smegma (the oily product of the glands) to build up. If build-up occurs to a great degree within these folds, soreness can develop, and result in erection and/or ejaculatory dysfunction. Stallions should be checked and cleaned regularly during the breeding season to avoid this problem. Warm water is sufficient for washing the stallion. Detergents and disinfectants should be avoided as they remove the natural microflora present on the stallion's penis. Removal of the natural microflora allows for potentially pathogenic organisms to take up residence.

During erection, the erectile tissue of the penis (corpus cavernosum and corpus spongiosum) becomes engorged with blood. The size and diameter of the penis shaft increases about 50 percent during an erect state. However, the glans penis, which does not have a tough connective tissue covering as found on the shaft, increases approximately 30-400 percent during erection. The increased size of the glans penis is often referred to as 'flowering' or 'belling.' For stallions enrolled in an artificial insemination program, the tremendous increase in size of the glans penis must be kept in mind when preparing the artificial vagina (AV). Excessive pressure and/or temperature of the AV might prevent flowering and induce pain or discomfort to the stallion to the point that the stallion fails to ejaculate. Likewise, failure of the stallion to bell up when servicing the AV would be indicative of improper stimulation and subsequent failure to ejaculate.

EJACULATION

During ejaculation, spermatozoa are released from the tail of the epididymis and are moved via muscular contractions through the ductus deferens into the pelvic urethra. Spermatozoa are mixed with secretions of the accessory sex glands during ejaculation. Collectively, the secretions and spermatozoa are referred to as semen. The fluid portion, consisting of testicular, epididymal, and accessory sex gland secretions, is referred to as seminal plasma. The role of seminal plasma is not fully understood. However, in addition to serving as a means to transport sperm through the male tract, the fluid is generally believed to contain buffers, nutrients and stabilizing factors for spermatozoa.

Seminal plasma volume can be controlled somewhat through sexual stimulation. It may be beneficial in artificial insemination programs to increase or decrease the ejaculate volume. Teasing the stallion can increase the ejaculate volume and lower spermatozoal concentration. It is not uncommon for stallions housed near "mare activity" to ejaculate large volumes with low concentration. Moving these stallions to an area away from "mare activity" may result in lower volumes with higher spermatozoal concentration. Similarly, stallions which characteristically ejaculate small volumes can be teased for longer periods of time to increase their volume. Note that teasing influences ejaculate volume and sperm concentration per milliliter of semen, not total sperm number per ejaculate.

Semen emitted during ejaculation in the stallion normally occurs in fractions. The first fraction emitted is normally referred to as the presperm fraction. It is generally believed to be of bulbo urethral origin, and thought to function in cleansing the urethra. The second function is referred to as the sperm-rich fraction. It contains approximately 45 percent of the ejaculate volume, 75 percent of the spermatozoa, and is predominantly of ampullar origin. The third fraction is referred to as the sperm-poor fraction and is primarily of vesicular origin. This fraction contains the gel portion which is normally filtered out and discarded during semen collection for artificial insemination. Collection of fractionated ejaculates with an open-ended artificial vagina is commonly used to harvest the sperm-rich fraction for use in cryopreservation programs. This technique eliminates the centrifugation process normally employed to concentrate spermatozoa, and may eliminate components of vesicular origin which are potentially harmful to spermatozoa during the freezing process.

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