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### Nursing Sci

### MHS

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### Sperm Transport in the Female Reproductive Tract

Sperm transport within the female reproductive tract is a cooperative effort between the functional properties of the sperm and seminal fluid on the one hand and cyclic adaptations of the female reproductive tract that facilitate the transport of sperm toward the ovulated egg. Much of the story of sperm transport in the female [reproductive system](/topics/biochemistry-genetics-and-molecular-biology/reproductive-system" \o "Learn more about Reproductive System from ScienceDirect's AI-generated Topic Pages) involves the penetration by the sperm of various barriers along their way toward the egg (see Fig. 14.7B).

During [coitus](/topics/biochemistry-genetics-and-molecular-biology/coitus" \o "Learn more about Coitus from ScienceDirect's AI-generated Topic Pages) in the human, semen is deposited in the upper ****vagina**** close to the cervix. The normal environment of the vagina is inhospitable to the survival of sperm, principally because of its low pH (<5.0). The low pH of the vagina is a protective mechanism for the woman against many sexually transmitted pathogens, because no tissue barrier exists between the vagina (outside) and the peritoneal cavity (inside). The acidic pH of the vagina is bacteriocidal and is the reflection of an unusual functional adaptation of the vaginal epithelium. Alone among the stratified squamous epithelia in the body, the cells of the vaginal lining contain large amounts of ****glycogen****. Anaerobic [lactobacilli](/topics/biochemistry-genetics-and-molecular-biology/lactobacillus" \o "Learn more about Lactobacillus from ScienceDirect's AI-generated Topic Pages) within the vagina break down the glycogen from shed vaginal epithelial cells, with the production of ****lactic acid**** as a byproduct. The lactic acid is responsible for the lowered [vaginal pH](/topics/biochemistry-genetics-and-molecular-biology/vagina-ph" \o "Learn more about Vagina pH from ScienceDirect's AI-generated Topic Pages).

Direct measurements have shown that within 8 seconds from the introduction of semen the pH of the upper vagina is raised from 4.3 to 7.2, creating an environment favorable for [sperm motility](/topics/biochemistry-genetics-and-molecular-biology/spermatozoon-motility" \o "Learn more about Spermatozoon Motility from ScienceDirect's AI-generated Topic Pages). Another rapid event is the coagulation of human semen through the actions of semogelin by a minute after coitus. The coagulative function is incompletely understood, but it may play a role in keeping sperm near the cervical os. Thirty to 60 minutes after it coagulates, [prostate-specific antigen](/topics/biochemistry-genetics-and-molecular-biology/prostate-specific-antigen" \o "Learn more about Prostate-Specific Antigen from ScienceDirect's AI-generated Topic Pages) (PSA), a [proteolytic enzyme](/topics/biochemistry-genetics-and-molecular-biology/peptide-hydrolases" \o "Learn more about Peptide Hydrolases from ScienceDirect's AI-generated Topic Pages), degrades the coagulated semen. Within the semen and altered vaginal fluids, the sperm have begun to swim actively. A critical element in sperm motility is the availability of [fructose](/topics/biochemistry-genetics-and-molecular-biology/fructose" \o "Learn more about Fructose from ScienceDirect's AI-generated Topic Pages), a nutrient provided by the seminal vesicles, within the semen. Because of their paucity of cytoplasm, spermatozoa require an external energy source. Unusually for most cells, spermatozoa have a specific requirement for fructose rather than glucose, the more commonly utilized carbohydrate energy source.

The next barrier facing sperm is the ****cervix****. The cervical entrance (os) is not only very small, but it is blocked by cervical mucus. During most times in the [menstrual cycle](/topics/biochemistry-genetics-and-molecular-biology/menstrual-cycle" \o "Learn more about Menstrual Cycle from ScienceDirect's AI-generated Topic Pages), cervical mucus is highly sticky (G mucus) and represents an almost impenetrable barrier to [sperm penetration](/topics/biochemistry-genetics-and-molecular-biology/spermatozoon-penetration" \o "Learn more about Spermatozoon Penetration from ScienceDirect's AI-generated Topic Pages). Around the time of ovulation, however, the estrogenic environment of the female reproductive system brings about a change in cervical mucus, rendering it more watery and more amenable to penetration by sperm (E mucus).

Considerable uncertainty surrounds the question of passage of sperm through the cervix. The swimming speed of human sperm in fluid is approximately 5 mm/min, so in theory, sperm could swim through the cervical canal in a matter of minutes or hours. In reality, some sperm have been found in the upper reaches of the uterine tubes within minutes of coitus. These pioneers are likely to have been swept up the female reproductive tract during [muscular contractions](/topics/biochemistry-genetics-and-molecular-biology/muscle-contraction" \o "Learn more about Muscle Contraction from ScienceDirect's AI-generated Topic Pages) occurring at the time of or shortly after coitus. Research on [rabbits](/topics/biochemistry-genetics-and-molecular-biology/leporidae" \o "Learn more about Leporidae from ScienceDirect's AI-generated Topic Pages) has indicated that most of these sperm have been damaged and would not be able to fertilize an egg. The functional status of early-arriving human sperm is not known. On the other end of the spectrum, viable sperm have been taken from the cervix as long as 5 days after coitus. Between these two extremes, over the course of hours or even days, most of the spermatozoa make their way through the cervical mucus and up the cervical canal and into the uterus, where even less is known about the course of sperm transport in the human. Whether or not sperm are stored in the cervix is still not entirely certain. Sperm transport into and through the uterus is assumed to be assisted by contractions of its thick smooth muscle walls. There may or may not be subtle influences that favor the transport of sperm toward the opening of the uterine tube that contains the ovulated egg.

Of the huge numbers of sperm that enter the female reproductive tract, almost all fail to reach the uterine tubes. The unsuccessful sperm are removed by the infiltration of white blood cells into the cavities of the vagina, cervix, and uterus. These cells, along with certain immunoglobulins, inactivate and degrade foreign invaders, in this case, the excess sperm. Fortunately, the uterine tubes are not subject to this sort of cellular infiltration.

The openings of the uterine tubes into the uterus (****uterotubal junction****) represent another barrier to sperm transport. With two uterine tubes and usually only one ovulated egg, any spermatozoon that enters the empty uterine tube is automatically doomed to reproductive failure. Roughly 10,000 or fewer sperm cells of the millions in the ejaculate enter the correct tube. These sperm cells collect in the lower part of the uterine tube and attach to the epithelium of the tube for about 24 hours.

Two critical events occur during this period of attachment. The first is called [capacitation](/topics/biochemistry-genetics-and-molecular-biology/capacitation" \o "Learn more about Capacitation from ScienceDirect's AI-generated Topic Pages), a reaction necessary for a spermatozoon to be able to fertilize an egg. The first phase of the capacitation reaction is the removal of cholesterol from the surface of the sperm. Cholesterol was introduced onto the sperm head to prevent premature capacitation. The next phase of capacitation is the removal of many of the [glycoproteins](/topics/biochemistry-genetics-and-molecular-biology/glycoproteins" \o "Learn more about Glycoproteins from ScienceDirect's AI-generated Topic Pages) that were deposited on the sperm head within the epididymis. After their removal, the spermatozoon is now capable of fertilizing an egg. It is likely that covering the sperm cells with glycoproteins and then cholesterol is done to prevent the sperm from prematurely attempting to fertilize other [somatic cells](/topics/biochemistry-genetics-and-molecular-biology/somatic-cell" \o "Learn more about Somatic Cell from ScienceDirect's AI-generated Topic Pages) that they encounter on their way to meeting the egg. Capacitation removes the molecular shield.

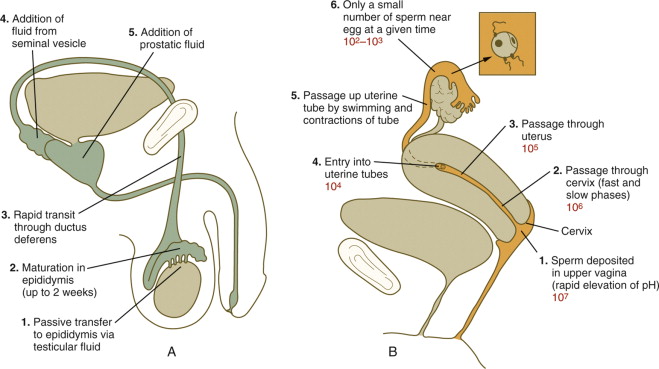
A second phenomenon occurring while the sperm are attached to the distal tubal lining is ****hyperactivation**** of the sperm. Hyperactivation is manifest by the increased vigor in their swimming movements and allows the sperm to break free from their binding with the tubal epithelial cells. Hyperactivated sperm are more efficient in making their way up the uterine tube and penetrating the coverings of the egg.

Once capacitated sperm break away from the tubal epithelium, they make their way up the uterine tube through a combination of their own swimming movements, [peristaltic contractions](/topics/biochemistry-genetics-and-molecular-biology/peristalsis" \o "Learn more about Peristalsis from ScienceDirect's AI-generated Topic Pages) of the smooth musculature of the tubal wall and the movement of tubal fluids directed by ciliary activity. In the upper third of the uterine tube, a few hundred sperm approach the ovulated egg. Only one of them out of the millions that left the male reproductive tract will attain is ultimate goal of fertilizing that egg.

### Sperm Transport

Sperm transport occurs in both the male reproductive tract and the female reproductive tract. In the male reproductive tract, transport of spermatozoa is closely connected with their structural and functional maturation, whereas in the female reproductive tract, it is important for spermatozoa to pass to the upper uterine tube, where they can meet the ovulated egg.

After spermiogenesis in the [seminiferous tubules](/topics/engineering/seminiferous-tubule" \o "Learn more about Seminiferous Tubule from ScienceDirect's AI-generated Topic Pages), the spermatozoa are morphologically mature but are nonmotile and incapable of fertilizing an egg (****Figure 2****). Spermatozoa are passively transported via testicular fluid from the seminiferous tubules to the caput (head) of the epididymis through the rete testis and the efferent ductules. They are propelled by fluid pressure generated in the seminiferous tubules and are assisted by smooth muscle contractions and ciliary currents in the efferent ductules. Spermatozoa spend about 12 days in the highly convoluted duct of the epididymis, which measures 6 m in the human, during which time they undergo [biochemical](/topics/engineering/biochemicals" \o "Learn more about Biochemicals from ScienceDirect's AI-generated Topic Pages) maturation. This period of maturation is associated with changes in the glycoproteins in the plasma membrane of the sperm head. By the time the spermatozoa have reached the cauda (tail) of the epididymis, they are capable of fertilizing an egg.



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Figure 2. Sperm transport in (a) the male and (b) the female reproductive tracts. In (b), numbers of spermatozoa typically found in various parts of the female reproductive tract are indicated in red.

On ejaculation, the spermatozoa rapidly pass through the ductus deferens and become mixed with fluid secretions from the seminal vesiclesand prostate gland. Prostatic fluid is rich in [citric acid](/topics/engineering/citric-acid" \o "Learn more about Citric Acid from ScienceDirect's AI-generated Topic Pages), [acid phosphatase](/topics/engineering/acid-phosphatase" \o "Learn more about Acid Phosphatase from ScienceDirect's AI-generated Topic Pages), zinc, and magnesium ions, whereas fluid of the seminal vesicle is rich in fructose (the principal energy source of spermatozoa) and prostaglandins. The 2–6 ml of ejaculate (semen, or seminal fluid) typically consists of 40–250 million spermatozoa mixed with alkaline fluid from the seminal vesicles (60% of the total) and acid secretion (pH 6.5) from the prostate (30% of the total). The pH of normal semen ranges from 7.2 to 7.8.

In the female reproductive tract, sperm transport begins in the upper vagina and ends in the ampulla of the uterine tube, where the spermatozoa make contact with the ovulated egg. During copulation, the seminal fluid is normally deposited in the upper vagina, where its composition and buffering capacity immediately protect the spermatozoa from the acid fluid found in the upper vaginal area. The acidic vaginal fluid normally serves a bactericidal function in protecting the cervical canal from pathogenic organisms. Within about 10 seconds, the pH of the upper vagina is increased from 4.3 to as much as 7.2. The buffering effect lasts only a few minutes in humans, but it provides enough time for the spermatozoa to approach the cervix in an environment (pH 6.0–6.5) optimal for sperm motility.

The next barriers that the sperm cells must overcome are the cervical canal and the cervical mucus that blocks it. Changes in intravaginal pressure may suck spermatozoa into the cervical os, but swimming movements also seem to be important for most spermatozoa in penetrating the cervical mucus.

The composition and viscosity of cervical mucus vary considerably throughout the menstrual cycle. Composed of cervical mucin (a glycoprotein with a high carbohydrate composition) and soluble components, cervical mucus is not readily penetrable. Between days 9 and 16 of the cycle, however, its water content increases, and this change facilitates the passage of sperm through the cervix around the time of ovulation; such mucus is sometimes called E mucus. After ovulation, under the influence of progesterone, the production of watery cervical mucus ceases, and a new type of sticky mucus, which has a much decreased water content, is produced. This progestational mucus, sometimes called G mucus, is almost completely resistant to sperm penetration.

There are two main modes of sperm transport through the cervix. One is a phase of initial rapid transport, by which some spermatozoa can reach the uterine tubes within 5–20 min of ejaculation. Such rapid transport relies more on muscular movements of the female reproductive tract than on the motility of the spermatozoa themselves. These early-arriving sperm, however, appear not to be as capable of fertilizing an egg as do those that have spent more time in the female reproductive tract. The second, slow phase of sperm transport involves the swimming of spermatozoa through the cervical mucus (traveling at a rate of 2–3 mm h− 1), their storage in cervical crypts, and their final passage through the cervical canal as much as 2–4 days later.

Relatively little is known about the passage of spermatozoa through the uterine cavity, but the contraction of uterine smooth muscle, rather than sperm motility, seems to be the main intrauterine transport mechanism. At this point, the spermatozoa enter one of the uterine tubes. According to some more recent estimates, only several hundred spermatozoa enter the uterine tubes, and most enter the tube containing the ovulated egg.

Once inside the uterine tube, the spermatozoa collect in the isthmus and bind to the epithelium for about 24 h. During this time, they are influenced by secretions of the tube to undergo the capacitation reaction. One phase of capacitation is the removal of cholesterol from the surface of the sperm. Cholesterol is a component of semen and acts to inhibit premature capacitation. The next phase of capacitation consists of removal of many of the glycoproteins that were deposited on the surface of the spermatozoa during their tenure in the epididymis. Capacitation is required for spermatozoa to be able to fertilize an egg (specifically, to undergo the acrosome reaction). After the capacitation reaction, the spermatozoa undergo a period of hyperactivity and detach from the tubal epithelium. Hyperactivation helps the spermatozoa to break free of the bonds that held them to the tubal epithelium. It also assists the sperm in penetrating isthmic mucus, as well as the corona radiata and the zona pellucida, which surround the ovum. Only small numbers of sperm are released at a given time.

On their release from the isthmus, the spermatozoa make their way up the tube through a combination of muscular movements of the tube and some swimming movements. The simultaneous transport of an egg down and spermatozoa up the tube is currently explained on the basis of peristaltic contractions of the uterine tube muscles. These contractions subdivide the tube into compartments. Within a given compartment, the gametes are caught up in churning movements that over 1 or 2 days bring the egg and spermatozoa together. Fertilization of the egg normally occurs in the ampullary portion (upper third) of the uterine tube. Estimates suggest that spermatozoa retain their function in the female reproductive tract for about 80 h.

### Preparation of Recipient Mares

During OT, sperm transport, [capacitation](/topics/veterinary-science-and-veterinary-medicine/capacitation" \o "Learn more about Capacitation from ScienceDirect's AI-generated Topic Pages), fertilization, and embryo development occur within the recipient’s reproductive tract; therefore, it is very important that a selection of good quality recipient mares be used in an OT program. Young mares (3 to 10 years) are selected after a complete clinical and reproductive examination. During the reproductive examination, it is important to evaluate the length of the broad ligaments to determine if the ovaries can be easily exposed during OT. Oocyte recipients can be cyclic or non-cyclic mares. Use of cyclic mares as oocyte recipients involves [estrous cycle](/topics/veterinary-science-and-veterinary-medicine/estrous-cycle" \o "Learn more about Estrous Cycle from ScienceDirect's AI-generated Topic Pages)synchronization of donor and recipient mares and the removal of the recipient’s oocytes to be sure that the pregnancy will result from fertilization of the donor oocyte. Recipient mares receive 2000 IU of hCG at the same time as the donors, and the recipient’s oocyte is collected approximately 24 hours after hCG administration. Only recipient mares from which an oocyte is collected are used as oocyte recipients. Use of non-cyclic recipients eliminates the need to synchronize donors and recipients and eliminates the need to retrieve the pre-ovulatory oocytes from the recipients before transfers. Non-cyclic recipients receive 3 mg of [estradiol](/topics/veterinary-science-and-veterinary-medicine/estradiol" \o "Learn more about Estradiol from ScienceDirect's AI-generated Topic Pages) benzoate daily for approximately 2 to 5 days before transfer. Following the estradiol treatment 200 mg per day of injectable [progesterone](/topics/veterinary-science-and-veterinary-medicine/progesterone" \o "Learn more about Progesterone from ScienceDirect's AI-generated Topic Pages) in oil or 0.044 mg/kg of oral [progestagen](/topics/veterinary-science-and-veterinary-medicine/progestagen" \o "Learn more about Progestagen from ScienceDirect's AI-generated Topic Pages)(Altrenogest), supplementation is required until OT. Regardless of whether the mares are cycling or not, progesterone supplementation must be continued for pregnancy maintenance until day 110 to 120. Although a [corpus luteum](/topics/veterinary-science-and-veterinary-medicine/corpus-luteum" \o "Learn more about Corpus Luteum from ScienceDirect's AI-generated Topic Pages) forms after aspiration of the preovulatory follicle,65 progesterone secretion can be delayed or reduced in cyclic mares. In non-cyclic mares, the absence of corpus luteum obviously requires progesterone supplementation.

Oocytes are transferred into the [oviduct](/topics/veterinary-science-and-veterinary-medicine/oviduct" \o "Learn more about Oviduct from ScienceDirect's AI-generated Topic Pages) of the recipient mares preferably by standing flank laparotomy. After sedation and local anesthesia, an incision is made between the last rib and the tuber coxae. Prior to OT the ovary and oviduct are exposed through the incision. The oocyte is loaded into a fire-polished glass pipette with a low volume of medium (<0.1 ml). The pipette is introduced approximately 3 cm into the infundibular end of the oviduct and the oocyte is gently deposited (Fig. 18-4). The ovary is returned into the [abdominal cavity](/topics/veterinary-science-and-veterinary-medicine/abdominal-cavity" \o "Learn more about Abdominal Cavity from ScienceDirect's AI-generated Topic Pages), and the muscle layers and skin are sutured separately. Recipients are routinely treated with parenteral [non-steroidal anti-inflammatory drugs](/topics/veterinary-science-and-veterinary-medicine/non-steroidal-anti-inflammatory-drugs" \o "Learn more about Non-Steroidal Anti-Inflammatory Drugs from ScienceDirect's AI-generated Topic Pages) and broad spectrum antibiotic for 5 to 7 days after surgery.

### Basic Information

#### Definition

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Ejaculation is the process of sperm transport from the epididymis to the urethral [meatus](/topics/veterinary-science-and-veterinary-medicine/meatus" \o "Learn more about Meatus from ScienceDirect's AI-generated Topic Pages), resulting in expulsion of semen. Ejaculation is divided in two phases: seminal emission, which occurs at high arousal, and propulsatile ejaculation.

#### Synonyms

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[Aspermia](/topics/veterinary-science-and-veterinary-medicine/aspermia" \o "Learn more about Aspermia from ScienceDirect's AI-generated Topic Pages), anejaculation, retrograde ejaculation, urospermia, [premature ejaculation](/topics/veterinary-science-and-veterinary-medicine/premature-ejaculation" \o "Learn more about Premature Ejaculation from ScienceDirect's AI-generated Topic Pages)

#### Epidemiology

##### **Species, Age, Sex**

Males of any age

##### **Associated Conditions and Disorders**

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[Musculoskeletal disorders](/topics/veterinary-science-and-veterinary-medicine/musculoskeletal-disorder" \o "Learn more about Musculoskeletal Disorder from ScienceDirect's AI-generated Topic Pages) (sore back, lameness, degenerative joint, lameness after breeding, [myositis](/topics/veterinary-science-and-veterinary-medicine/myositis" \o "Learn more about Myositis from ScienceDirect's AI-generated Topic Pages), laminitis)

•

Neurologic diseases (EPM)

•

Vascular lesions (aortoiliac thrombosis)

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Cystic remnant of Müllerian ducts (uterus masculinus)

#### Clinical Presentation

##### **Disease Forms/Subtypes**

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Ejaculation failure (aspermia, anejaculation): The most common cause of ejaculatory dysfunction. It is an intermittent or continuous failure of emission of semen and ejaculation in spite of normal sexual arousal and persistent mounting and thrusting.

•

Sperm accumulation syndrome (spermiostasis/spermastasis): Abnormal accumulation of sperm within the ductal system.

•

Urospermia: Emission of variable quantities of urine during ejaculation.

•

Premature ejaculation: Very rare affliction in which ejaculation occurs before adequate insertion.

•

Retrograde ejaculation: Process by which semen passes backward through the bladder neck into the bladder. It can be partial or total.

##### **History, Chief Complaint**

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Poor breeding performance

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Difficulty in collecting semen

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Poor [semen quality](/topics/veterinary-science-and-veterinary-medicine/semen-quality" \o "Learn more about Semen Quality from ScienceDirect's AI-generated Topic Pages) (intermittent or permanent)

##### **Physical Exam Findings**

•

Possibly none; findings are variable depending on cause.

•

Musculoskeletal or neurologic dysfunctions during mating or semen collection, such as failure to couple squarely and thrust; asymmetric hind limb weight bearing and thrusting; lateral instability; falling during thrusting or dismount; reluctance to mount or dismount; early dismount.

•

Acute or chronic sources of pain affecting the urogenital tract (eg, [epididymitis](/topics/veterinary-science-and-veterinary-medicine/epididymitis" \o "Learn more about Epididymitis from ScienceDirect's AI-generated Topic Pages), scrotal inflammation).

•

Acute or chronic lesions of the penis.

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Ultrasonographic examination of:

○

The accessory sex glands could show dilated (fluid filled) and/or hyperechoic areas of the ampullae.

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Arteries: For aortoiliac thrombosis.

##### **Etiology and Pathophysiology**

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Ejaculation failure:

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Acute or chronic pain of musculoskeletal origin (back pain, painful hind limb, lameness)

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Urogenital tract problem (pain of the bladder, the penis, testis, or accessory sex gland)

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Neurologic dysfunction (penile nerve damage, “tail nerving,” incomplete spinal injury)

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Vascular problems (aortoiliac thrombosis)

○

Psychogenic causes, such as poor handling (excessive punishment such as overuse of the chain shank or bit, overuse of the [stallion](/topics/veterinary-science-and-veterinary-medicine/stallion" \o "Learn more about Stallion from ScienceDirect's AI-generated Topic Pages), poor or inappropriate breeding environment (unstable phantom, slippery breeding shed floor), which induces pain, fear, or unpleasant experience.

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Sperm accumulation syndrome: Stallions with large testicles and high daily sperm production that are sexually rested for long periods. The sperm has a lower motility, reduced longevity, and poorer morphology.

•

Urospermia: Unknown cause. Associated conditions include:

○

Neurologic dysfunction (cauda equina syndrome or [equine herpesvirus-1](/topics/veterinary-science-and-veterinary-medicine/equine-herpesvirus-1" \o "Learn more about Equine Herpesvirus 1 from ScienceDirect's AI-generated Topic Pages) infection)

○

Poor or inadequate closure of the bladder neck

○

Neoplastic changes

○

Sorghum toxicosis

○

Sequelae of fractures and osteomyelitis

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Premature ejaculation: Unknown cause

•

Retrograde ejaculation: Extremely rare

○

Impairment of the muscles or nerves of the bladder neck prohibit closure during ejaculation

○

Trauma or surgery of the bladder, prostate, or pelvic urethra

○

Congenital defect in the urethra or bladder

○

Disease affecting the nervous system

In the oviduct, the integrity of oocyte and sperm transport, [fertilization](/topics/biochemistry-genetics-and-molecular-biology/fertilization" \o "Learn more about Fertilization from ScienceDirect's AI-generated Topic Pages), and early embryonic [ontogenesis](/topics/biochemistry-genetics-and-molecular-biology/ontogeny" \o "Learn more about Ontogeny from ScienceDirect's AI-generated Topic Pages) is essential for successful reproduction. Up to now, most of the knowledge on oocyte and sperm transport, [gamete](/topics/biochemistry-genetics-and-molecular-biology/gamete" \o "Learn more about Gamete from ScienceDirect's AI-generated Topic Pages) interaction and [embryonic development](/topics/biochemistry-genetics-and-molecular-biology/embryogenesis" \o "Learn more about Embryogenesis from ScienceDirect's AI-generated Topic Pages) has in most cases been gained exclusively by in vitro studies. In addition, especially the mechanisms of gameto–maternal interaction and embryo–maternal communication in the oviduct are still unknown. Recent techniques of live [cell imaging](/topics/biochemistry-genetics-and-molecular-biology/cellular-imaging" \o "Learn more about Cellular Imaging from ScienceDirect's AI-generated Topic Pages) and digital videomicroscopy allow for the first time to provide actual new insights in the mechanisms of sperm transport, sperm storage, [oocyte transport](/topics/biochemistry-genetics-and-molecular-biology/oocyte-transport" \o "Learn more about Oocyte Transport from ScienceDirect's AI-generated Topic Pages), fertilization, gameto–maternal interaction and embryo–maternal crosstalk under near in vivoconditions. Detailed knowledge of these important events in the oviduct is the prerequisite to develop new therapeutic concepts for subfertility and infertility and to increase the success rates of the actual techniques of assisted reproduction (ART). Additionally the effects of drugs and hormones used in ART can be effectively studied using a functional oviductal epithelium. The guidelines for live cell imaging in the oviduct presented here should enable researches to establish a functional digital analysis system which allows to study physiological and pathological events in the oviduct under near in vivo conditions.

### D Sperm transport and storage in the female reproductive tract

Although there are no data available on the dynamics of sperm transport in the female reproductive tract in [monotremes](/topics/biochemistry-genetics-and-molecular-biology/monotreme" \o "Learn more about Monotreme from ScienceDirect's AI-generated Topic Pages), nor on the barriers to sperm passage, sperm storage has been suggested to occur in the [oviducts](/topics/agricultural-and-biological-sciences/oviducts" \o "Learn more about Oviducts from ScienceDirect's AI-generated Topic Pages) of the short-beaked echidna (Griffith 1978) as an explanation for an unusually long [gestation period](/topics/agricultural-and-biological-sciences/gestation-period" \o "Learn more about Gestation Period from ScienceDirect's AI-generated Topic Pages) in one individual. Hibernation-related sperm storage has also been hypothesized for the echidna by Geiser and Seymour (1989), but more recent observations from Beard et al.(1992) were more consistent with [copulation](/topics/agricultural-and-biological-sciences/copulation" \o "Learn more about Copulation from ScienceDirect's AI-generated Topic Pages)occurring post-hibernation. Sperm storage in the female has also been suggested for the platypus by Griffith (1978) from observations by Flyn and Hill (1939) of [spermatozoa](/topics/agricultural-and-biological-sciences/spermatozoa" \o "Learn more about Spermatozoa from ScienceDirect's AI-generated Topic Pages) in the uterus and uterine glands of a female with oocytes that were not yet developed.

### EPIDIDYMAL FUNCTIONS

The [epididymis](/topics/agricultural-and-biological-sciences/epididymis" \o "Learn more about Epididymis from ScienceDirect's AI-generated Topic Pages) is far more than a passive organ, with functions including both sperm transport and maturation. [Spermatozoa](/topics/agricultural-and-biological-sciences/spermatozoa" \o "Learn more about Spermatozoa from ScienceDirect's AI-generated Topic Pages)leaving the [testis](/topics/agricultural-and-biological-sciences/testes" \o "Learn more about Testes from ScienceDirect's AI-generated Topic Pages) lack both the ability to survive in the female tract and to achieve unassisted fertilization. These capabilities are acquired in the epididymis. Other epididymal functions include the (1) energy-efficient storage of sperm while maintaining sperm fertility; (2) intermixing of recently formed and older [spermatozoa](/topics/agricultural-and-biological-sciences/spermatozoa" \o "Learn more about Spermatozoa from ScienceDirect's AI-generated Topic Pages) to provide a temporal spectrum of optimal sperm function, and (3) changing sperm attributes and environment to permit survival and ensure fertilizing capability within the female tract.7

Immotile spermatozoa are carried into the lumen of the [seminiferous tubule](/topics/agricultural-and-biological-sciences/seminiferous-tubules" \o "Learn more about Seminiferous Tubules from ScienceDirect's AI-generated Topic Pages) following separation of their connections to [Sertoli cells](/topics/agricultural-and-biological-sciences/sertoli-cell" \o "Learn more about Sertoli Cell from ScienceDirect's AI-generated Topic Pages). Most of the residual [cytoplasm](/topics/agricultural-and-biological-sciences/cytoplasm" \o "Learn more about Cytoplasm from ScienceDirect's AI-generated Topic Pages) is retained by the Sertoli cell, although some remains attached to the spermatozoa (as cytoplasmic droplets). Initial transport into the [rete testis](/topics/agricultural-and-biological-sciences/rete-testis" \o "Learn more about Rete Testis from ScienceDirect's AI-generated Topic Pages)and caput epididymidis seems to be dependent upon fluid secreted by Sertoli cells. Once into the [efferent ducts](/topics/veterinary-science-and-veterinary-medicine/efferent-ducts" \o "Learn more about Efferent Ducts from ScienceDirect's AI-generated Topic Pages), sperm movement is facilitated by ciliated [epithelial cells](/topics/agricultural-and-biological-sciences/epithelial-cells" \o "Learn more about Epithelial Cells from ScienceDirect's AI-generated Topic Pages) (within the ducts) as well as by smooth [muscle contractions](/topics/agricultural-and-biological-sciences/muscle-contraction" \o "Learn more about Muscle Contraction from ScienceDirect's AI-generated Topic Pages). The efferent ducts and initial segment of the caput epididymidis resorb most fluid and protein emanating from the testis and secrete new compounds.

Sperm maturation occurs within the caput and corpus of the epididymis with this process requiring the coordinated secretion of specialized enzymes and proteins. During this process, changes occur in the sperm DNA-protein complex, [plasma membrane](/topics/agricultural-and-biological-sciences/plasma-membrane" \o "Learn more about Plasma Membrane from ScienceDirect's AI-generated Topic Pages), [mitochondria](/topics/agricultural-and-biological-sciences/mitochondrion" \o "Learn more about Mitochondrion from ScienceDirect's AI-generated Topic Pages), axonemal complex, plasma and acrosomal membranes, and sperm surface characteristics.7

As spermatozoa progress through the epididymis, they achieve progressive motility, the cytoplasmic droplet migrates from the proximal to the distal position on the sperm midpiece, and seminal fluids are resorbed and exchanged. Heat stress can adversely affect epididymal function. The epididymis, particularly the tail region, acts as a storage region for sperm, such that a mature [Holstein](/topics/agricultural-and-biological-sciences/holstein" \o "Learn more about Holstein from ScienceDirect's AI-generated Topic Pages)bull may have epididymal reserves representing the equivalent of 6 or 7 days of daily sperm output. Most sperm that are not ejaculated are voided in urine, with a small proportion resorbed by the male tract. Some evidence exists for selective resorption of spermatozoa within the epididymis.

Sperm are transported from the cauda epididymis to the [urethra](/topics/agricultural-and-biological-sciences/urethra" \o "Learn more about Urethra from ScienceDirect's AI-generated Topic Pages) in the [ductus deferens](/topics/agricultural-and-biological-sciences/ductus-deferens" \o "Learn more about Ductus Deferens from ScienceDirect's AI-generated Topic Pages) (vas deferens) via muscle contractions that are strongest during precoital stimulation. The terminal portions of the ductus deferens expand to form the ampullae (each approximately 10 × 1.5 cm in adult bulls). These ampullae act as minor sperm storage areas and they also secrete fructose and [citric acid](/topics/agricultural-and-biological-sciences/citric-acid" \o "Learn more about Citric Acid from ScienceDirect's AI-generated Topic Pages) into the [seminal plasma](/topics/agricultural-and-biological-sciences/seminal-plasma" \o "Learn more about Seminal Plasma from ScienceDirect's AI-generated Topic Pages). The ductus deferens open (via the ampullae) into the cranial portion of the pelvic urethra. The vesicular glands (or seminal vesicles) also open into the pelvic urethra. These glands provide much of the fluid component of the bull ejaculate, as well as sperm nutrients and semen buffers. The vesicular glands are lobulated organs, approximately 10 to 15 cm in length and 2 to 4 cm in diameter in mature bulls. The [prostate gland](/topics/agricultural-and-biological-sciences/prostate-gland" \o "Learn more about Prostate Gland from ScienceDirect's AI-generated Topic Pages), consisting of a relatively small body and larger disseminate region, produces 25% to 40% of seminal volume as well as semen odor. The [bulbourethral glands](/topics/agricultural-and-biological-sciences/bulbourethral-gland" \o "Learn more about Bulbourethral Gland from ScienceDirect's AI-generated Topic Pages) of the bull each open into the pelvic urethra at the ischial arch. The urethra is an elongated tube extending from the bladder to the tip of the penis. It is surrounded by the urethralis muscle, which contracts strongly during ejaculation

### A love–hate relationship?

Sexually reproducing females need viable sperm to reproduce. During ejaculation and some phases of sperm transport through the female reproductive tract, sperm are subjected to physical stresses and may sustain oxidative damage to their [plasma membrane](/topics/agricultural-and-biological-sciences/plasma-membrane" \o "Learn more about Plasma Membrane from ScienceDirect's AI-generated Topic Pages) lipids. Because sperm generally are terminally differentiated cells without an active nucleus and transcription apparatus, they lack the full repertoire of repair mechanisms available to [somatic cells](/topics/agricultural-and-biological-sciences/somatic-cells" \o "Learn more about Somatic Cells from ScienceDirect's AI-generated Topic Pages) or oocytes. Thus, and given that there may be a lengthy interval between [insemination](/topics/agricultural-and-biological-sciences/insemination" \o "Learn more about Insemination from ScienceDirect's AI-generated Topic Pages) and fertilization, the female must protect sperm against degenerative changes. Indeed, females exhibit a variety of adaptations for sustaining sperm viability.

It is thus initially paradoxical to recognize that the female reproductive tract may also present an environment that is somewhat unfavorable to, and thus selective on, sperm. Conditions precluding some sperm reaching eggs may include (i) active sperm ejection by females (e.g., Pizzari & Birkhead 2000), (ii) physical barriers (e.g., cervix, long ducts), (iii) chemical barriers (e.g., low pH and viscous mucus), and (iv) leukocytic/phagocytotic responses within the female (Suarez 2006). Consequently, in many species only a small proportion of the inseminated sperm ever have the opportunity to encounter an egg. For example, of the 189 million sperm in a typical human ejaculate (Handelsman et al. 1984), only a few thousand ever reach the [oviduct](/topics/agricultural-and-biological-sciences/oviducts" \o "Learn more about Oviducts from ScienceDirect's AI-generated Topic Pages) (Suarez & Pacey 2006). In birds, typically fewer than 2% of inseminated sperm even reach a female's sperm-storage tubules. However, this is not universal, as insome species females can be highly efficient in their sperm use (

Four non-mutually exclusive hypotheses have been proposed to explain the evolution of a female reproductive tract that is selective on sper these in turn may explain the complex and evolutionarily dynamic nature of EFIs. First, an environment that is selective on sperm may be a by-product of safeguards against parasites, bacterial infections and other pathogens that may enter the female reproductive tract, particularly at the time of mating. Second, ‘challenges’ to sperm may be adaptations to discriminate against sperm that have abnormal morphology, weak motility or are otherwise unfit for fertilization. Third, high sperm mortality and the consequent presence of few sperm at the site of fertilization may benefit females by reducing the risk of [polyspermy](/topics/agricultural-and-biological-sciences/polyspermy" \o "Learn more about Polyspermy from ScienceDirect's AI-generated Topic Pages). Fourth, conditions of the female tract may be sexually selected in two ways. (i) By posing challenges to sperm, females may ensure that their eggs are fertilized by the ‘best’ sperm, or by sperm from the ‘best’ males (or are not fertilized by ‘poor’ sperm) (see also Eberhard 1996; Birkhead 1998a; Section 7.5). (ii) Alternatively, sexual conflict over paternity will favor male adaptations (e.g., seminal protein and sperm traits) that increase the probability of a given male's sperm being usedover those from other males. To the extent that male adaptations to bias paternity are harmful to females, there will be selection for female adaptations that provide resistance to them (Parker 1979; Holland & Rice, 1998; Chapman et al. 2003; Arnqvist & Rowe 2005). The first and fourth hypotheses are especially likelytodrive rapid and pervasive diversification of EFIs, as both [pathogen/host interactions](/topics/agricultural-and-biological-sciences/host-pathogen-interaction" \o "Learn more about Host-Pathogen Interaction from ScienceDirect's AI-generated Topic Pages)and sexual conflict traits can enter into arms races or perpetual coevolutionary cycles.

Rapid evolutionary diversification of [reproductive traits](/topics/agricultural-and-biological-sciences/reproductive-traits" \o "Learn more about Reproductive Traits from ScienceDirect's AI-generated Topic Pages) has largely been attributed to sexually antagonistic [coevolution](/topics/agricultural-and-biological-sciences/coevolution" \o "Learn more about Coevolution from ScienceDirect's AI-generated Topic Pages) (e.g., Arnqvist et al. 2000; Swanson et al. 2001b). In practice, however, it is extremely difficult to discriminate this process from more traditional, ‘cooperative’ models (e.g., good genes and runaway sexual selection) for the evolution of reproductive traits (Pizzari & Snook 2003; Rowe et al. 2003; Arnqvist & Rowe 2005; Kokko et al. 2006). These different selection pressures can be acting simultaneously to varying degrees and differentially over time (Arnqvist & Rowe 2005). Conflict between the sexes isexpected to be ubiquitous among species that are not strictly monogamous (Rice 1998), but so is cooperation between the sexes. For example, it may be advantageous to females to use males as ‘hormone-delivery systems’ for controlling some aspects of their postmating physiology. The evolution in [Drosophila](/topics/agricultural-and-biological-sciences/drosophila" \o "Learn more about Drosophila from ScienceDirect's AI-generated Topic Pages) [melanogaster](/topics/agricultural-and-biological-sciences/melanogaster" \o "Learn more about Melanogaster from ScienceDirect's AI-generated Topic Pages) of male seminal prteins (‘Acps’; see below) that stimulate [oogenesis](/topics/agricultural-and-biological-sciences/oogenesis" \o "Learn more about Oogenesis from ScienceDirect's AI-generated Topic Pages) and ovulation in females, for instance, may mean that females only produce large numbers of eggs after mating when there will be sperm to fertilize them and/or that males manipulate female reproductive physiology to their own benefit and at a cost to females. Thus, cooperation and conflict are both likely to be potent forces shaping the evolution of EFI traits.

### Breeding Management of Superovulated Ewes

[Superovulation](/topics/agricultural-and-biological-sciences/superovulation" \o "Learn more about Superovulation from ScienceDirect's AI-generated Topic Pages) affects the dynamics of [estrus](/topics/agricultural-and-biological-sciences/estrus" \o "Learn more about Estrus from ScienceDirect's AI-generated Topic Pages), including time of onset and duration as well as sperm transport. All these factors affect fertilization rates and subsequent recovery of quality embryos. The optimal ram-to-ewe ratio for breeding superovulated [ewes](/topics/agricultural-and-biological-sciences/ewes" \o "Learn more about Ewes from ScienceDirect's AI-generated Topic Pages) is 1 : 3 during the normal breeding season and 1 : 2 for out of season. The ram should not be allowed with the ewes until 36 hours after [progestin](/topics/agricultural-and-biological-sciences/progestin" \o "Learn more about Progestin from ScienceDirect's AI-generated Topic Pages) removal even though some will show estrus as soon as 18 to 24 hours after withdrawal.

As an alternative to natural mating, laparoscopic AI has been shown to increase fertilization rates. Recent work suggests that embryo recovery rates may be decreased in a laparoscopic AI program, but breeding 60 hours after progestin removal has been shown to maximize embryo fertilization and recovery rates. Administration of [GnRH](/topics/veterinary-science-and-veterinary-medicine/gonadotropin-releasing-hormone" \o "Learn more about Gonadotropin-Releasing Hormone from ScienceDirect's AI-generated Topic Pages) 30 or 36 hours after eCG or FSH respectively has been reported to improve the yield of fertilized ova from both naturally and laparoscopically bred ewes.