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REVIEW [REVISIÓN]

# THE PHYSIOLOGY AND ECOPHYSIOLOGY OF EJACULATION

# [FISIOLOGÍA Y ECOFISIOLOGÍA DE LA EYACULACIÓN]

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## ABSTRACT

Different studies dealing with ejaculation view this process as a part of the male copulatory behavior. Some of them explain ejaculation as the consequence of a neuroendocrine feedback loops or from a purely anatomical perspective. The goal of the present review is to discuss the traditional and novel themes related to the biology of ejaculation. The text begins with the description of the behavioral motor patterns that lead to ejaculation. The anatomo-physiological mechanisms are explained under the notion that ejaculation is more than genitals and an excurrent duct system; thus it is also included the participation of the striated perineal musculature. Although ejaculation is a sexual spinal reflex, it is inhibited tonically by supraspinal structures. Such supraspinal modulation may explain the prudent sperm allocation, by which males adjust the number of sperm per ejaculate while copulating under distinct competitive scenarios. In some mammals, ejaculate components facilitate seminal coagulation, an adaptation that may increase the male reproductive fitness. Finally, there is a reflection of the so-called human ejaculatory disturbances, which from an ecophysiolgical perspective could represent advantages instead of sexual malfunction as are recognize under the medical view.

**Keywords:** Copulatory behavior; copulatory reflexes; disorders of ejaculation; prudent sperm allocation; seminal characteristics; sexual reflexes; sperm competition; sperm transport.

## RESUMEN

Diferentes estudios enfocados en la eyaculación, consideran a este proceso como parte de la conducta copulatoria masculina. Algunos de ellos explican la eyaculación como la consecuencia de una retroalimentación neuroendócrina o desde una perspectiva puramente anatómica. El objetivo de la presente revisión es discutir los temas tradicionales y novedosos relacionados con la biología de la eyaculación. El texto inicia con la descripción de los patrones motores copulatorios que conducen a la eyaculación. Se explican los mecanismos anátomo-fisiológicos considerando que la eyaculación es más que genitales y un sistema de ductos excurrentes; entonces también se incluye la participación de la musculatura perineal estriada. Aunque la eyaculación es un reflejo sexual espinal, está inhibido tónicamente por estructuras supraespinales. Tal modulación supraespinal puede explicar el reparto espermático conveniente, por el cual los machos ajustan el número de espermatozoides por eyaculado al copular en distintos escenarios competitivos. En algunos mamíferos, los componentes del eyaculado facilitan la coagulación del semen, una adaptación que puede incrementar el éxito reproductivo del macho. Finalmente, se reflexiona sobre los llamados desórdenes eyaculatorios humanos, que desde la perspectiva ecofisiológica podrían representar ventajas en lugar de disfunciones sexuales como son reconocidas desde el punto de vista médico

**Palabras clave:** Conducta copulatoria; reflejos copulatorios; desórdenes de la eyaculación; reparto espermático conveniente; características seminales; reflejos sexuales; competencia espermática; transporte espermático.

## INTRODUCTION

Ejaculation in mammals is a male sexual function design to inseminate the female. This ephemeral but essential process occurs when the male reaches the ejaculatory threshold during the copulatory encounter. In the present text ejaculation is analyzed in an integrative view, from proximal mechanisms to ultimate explanations. Then ejaculation is considered form a behavioral to ecophysiological perspectives.

## COPULATORY BEHAVIOR: THE EJACULATORY PRELUDE

Male sexual behavior comprises activities aimed at inseminating the female and fertilizing her ova. In general, two components are accepted to constitute this sex behavior. The first component referred to as sexual drive, *libido*, courtship or appetitive aspect involves the behavioral expression used by males to gain access to the female (*e.g.*, fighting for territory, advertising his physical attributes or providing food to females). The second component is known as performance, potency or consummatory aspect, and corresponds when copulation occurs. Males spent much more time and energy seeking for copulation than the actual time and energy used to copulate (Sachs and Meisel, 1988).

### Copulatory motor patterns and copulatory genital responses

The male copulatory behavior is expressed as motor patterns commonly organized in series of mounts, intromissions and ejaculation. In almost all mammals, the male mounts the female dorsally and from the rear. Males' mounts features pelvic movements (*i.e.*, thrusts) and flank palpation (Sachs and Garinello, 1978). Intromission occurs when the penis enters the vagina following a mount. Penile insertion may entail only a brief genital contact with immediate ejaculation (ungulates; Bermant *et al.*, 1969; Lott, 1981), it may consist of a single long connection (canids; Beach, 1969) or it may be an extended series of brief genital contacts as in before ejaculation is reached (rodents; Larsson, 1956). Ejaculation occurs when the inserted penis into the vagina expel seminal fluid *via* the urethral *meatus*. Ejaculation in male rats is the culmination of vigorous intravaginal pelvic thrusting accompanied by the arching of the male's spine and the lifting of his forepaws off the female prior to withdrawal. After ejaculation, the male dismount is followed by penis auto-grooming (Orbach, 1961; Lucio and Tlachi-López, 2008).

There are two genital responses during copulation, the penile erection that occurs during intromission and the seminal expulsion observed during ejaculation. Because both reflexes are difficult to assess and study during copulation, an *ex copula* stimulation protocol has been devised in rats. During these tests, erections are elicited by retracting the penile sheath while the male is kept in a supine position (Hart, 1968). The *ex copula* and *in copula* penile erections are similar in physiological terms (Hart, 1968; Holmes *et al.*, 1991). However, the temporal pattern of penile reflexes differs between natural and *ex copula* erections (Hart, 1968). Three gradations of erection can be observed: a) tumescence and elevation of the penile body without glans erection, b) intense erection of the glans "cup" and of the penile body, and c) anteroflexions of the penis due to the straightening of the penile body. During copulation cup formation is necessary for depositing the semen into the vagina, where it coagulates to form a solid seminal plug. Without this plug, much of the semen leaks out of the vagina and pregnancy rarely occurs (Sachs, 1982). These penile responses are present in "neutrally" intact rat males (Dusser de Barenne and Koskoff, 1932; Hart, 1968). Also, penile reflexes may be elicited from spinally transected humans (Zeitlin *et al.*, 1957). This indicates that penile reflexes are organized substantially at the spinal level. Reflexes are, nonetheless, subjected to considerable supra-spinal control (Beach, 1967).

Seminal expulsion refers to the forceful discharge of semen from the prostatic urethra through the urethral *meatus*. Ejaculation is elicited by urethral distention and results from the clonic contraction of the ischiocavernosus and bulbocavernosus muscles in response to the rhythmic firing of the cavernous nerve. This response is called the urethrogenital reflex and it can be observed in rats that have high spinal transection. A cluster of serotonergic neurons in the brain stem is implicated in the descending inhibition of spinal sexual reflexes (Marson and McKenna, 1990). The urethrogenital reflex is used as a model to study penile erection and ejaculation (McKenna *et al.*, 1991).

## EJACULATION: THE MALE´S AIM

Ejaculation is defined as the expulsion of seminal fluid from the urethral *meatus*. It involves coordinated series of reflexes activated during its two phases: emission and expulsion.

Seminal emission refers to the secretion of seminal plasma from the accessory sexual glands as the results of the peristaltic contraction of their smooth muscles; the transferring of seminal plasma and spermatozoa located into the epididymis cauda into the urethra then ensues. Thus, this process involves secretion of seminal plasma from epithelial cells and the accessory sexual glands, as well as contraction of the vas deferens to move seminal plasma and spermatozoa to the proximal urethra. Simultaneously to these parasympathetic and sympathetic actions, the urethral smooth muscles contract until closing the bladder´s neck preventing, under normal circumstances, retrograde ejaculation.

Once emission is completed, the ejaculate is ready to be expelled through the urethra. Seminal expulsion then occurs when the semen is rapidly and forcefully advanced forward along the urethra and spring out through the penile *meatus*. Adequate propulsion of semen requires the coordinated contraction of the external urethral sphincter and the bulbocavernosus, the striated muscles surrounding the urethra. Contraction of other perineal and pelvic muscles adjacent to the base of the penis, such as the ischiocavernosus and pubococcygeus muscles also contribute during seminal expulsion (Shafik *et al*., 2005). In humans, ejaculation is associated with what has been called orgasm; a subjective pleasurable feeling reported by men. Although we have no certainty of the existence of orgasms in other mammals, there are some studies that suggest that ejaculation of others mammals is also associated with reward (Kippin and Pfaus, 2001).

Rats present several accessory glands (seminal vesicles, coagulant glands, prostate and bulbourethral glands) whose secretion constitutes a significant fraction of the expelled semen during the ejaculation. During *ex copula* tests, seminal expulsion occurs occasionally. In anaesthetized animals, however, semen emission and expulsion may be elicited by electrical stimulation of the intermesenteric nerves (Bernabe *et al*., 2007) or by systemic administration of P-chloroamphetamine, an amphetamine derivative that releases catecholamines and serotonin from monoaminergic nerve terminals (Clement *et al*., 2006). With regard to the seminal expulsion from the urethra, it has been suggested that the rhythmic contraction of the urethral striated musculature is induced by the activation of the pressure urethral receptors. In agreement with this idea is the fact that increased urethral pressure induced contraction of the ischiocavernosus and bulbocavernosus muscles in man and in rats (McKenna *et al*., 1991). However, this notion is in conflict with evidence showing the triggering of expulsion in absence of seminal fluids within the prostatic urethra or after urethral anesthesia (Holmes and Sachs, 1991).

## Ejaculatory structures and ejaculatory reflex

In mammals, the male reproductive organs consist of the penis, two testes, two epididymides, accessory sexual glands with its ducts and the urethra. The penis is a copulatory organ composed of three sections; glans penis, body and root of the penis. The body is made up of three cylindrical bodies of erectile tissue, the paired *corpora cavernosa* and the centrally located *spongiosum* body, each one surrounded by the tunica *albuginea* (Hsu *et al*., 2004 ). The three bodies arise from the root of the penis in which skeletal muscle structures and the tunica *albuginea* completely surround smooth muscle structures; they intermingle with fibrous tissue to form the sinusoids wall (Hsu *et al*., 2004).The distal portion of the *spongiosum* body is expanded and becomes the glans of the penis, covered by the foreskin.

The testes produce spermatozoa and achieve glandular function secreting male sexual hormones such as testosterone (Setchell *et al.,* 1994). In adulthood the testicles, surrounded by the cremaster, rest into the scrotum. The epididymides are tubular coiled structures in close anatomical relation to the testes tubules. There, spermatozoa are stored and periodically expelled to the deferent duct (Setchell *et al.*, 1994). In primates, each vas deferens is joined by accessory gland ducts to form a common duct, the ejaculatory duct which opens into the urethra.

Accessory sexual glands secrete most of the seminal plasma expelled during ejaculation. Although there is a significant variation between mammals with respect to the range of them, most of the species have prostate and bulbourethral glands (Setchell *et al.*, 1994).

The organs described above are mainly involved in semen storage and production. For the semen to be placed into the female reproductive tract is necessary to count with a propulsion system, strong and fast enough to expel the fluid. The smooth and striated muscle of the urethra fills this requirement.

The urethra achieves urinary and reproductive function. It is an elongated structure whose cranial region connects to the urinary bladder, the medial region transverse the pelvic diaphragm and its distal portion ran along the *corpus spongiosum* of the penis. The urethra is usually divided in four regions: prostatic, membranous, bulbar (*diverticulum* in rats) and *spongiosum* or penile (Ciner *et al*., 1996). The distal portion of the penile urethra expands to form the external urinary *meatus*. In men the ejaculatory ducts discharge the semen into the prostatic urethra while in other species such as the rat the ducts enter into the dorsal wall of the cranial region of the membranous urethra (Bierinx and Sebille, 2006; Lehtoranta *et al*., 2006).

Around half of the urethra is surrounded by striated muscles. In rats, the prostatic and membranous regions are surrounded by the external urethral sphincter, a muscle also named rabdosphincter and the bulbar urethra is surrounded by the bulbocavernosus muscle (Pacheco *et al.,* 2002). Adjacent to the bulbocavernosus muscle is the ischiocavernosus muscle (McKenna and Nadelhaft, 1986). The contraction of these muscles compresses the bulb of the *corpus spongiosum* and the penile *crura*. In men the external urethral sphincter in mainly composed of circular slow fibers (Gosling *et al*., 1981). In contrast, in rats most of the fibers are fast twitch (Bierinx and Sebille, 2006; Lehtoranta *et al*., 2006). Similarly to man, in rats the rostral fibers of the external urethral sphincter are circular. Other fibers nonetheless run diagonally and longitudinally (Cruz and Downie, 2005; Lehtoranta *et al*., 2006). This muscular organization suggests that the external urethral sphincter is a complex muscle whose contraction contributes to urethral continence and urine and semen expulsion.

## Spinal and supraspinal control of ejaculation

The precise nature of the afferent stimuli that trigger the process of ejaculation is unknown. It is thought, however, that somatosensory stimulation of genital structures plays a chief role. The knowledge of the neural circuitry controlling the genital tract has been mostly obtained from animal studies.

Although not all the neural pathways controlling ejaculation have been identified, it is currently accepted that seminal emission and expulsion result from the activation of afferent, efferent, somatic, sympathetic and parasympathetic fibers (Clement *et al*., 2006). Accordingly, axons innervating the penis, foreskin and perineal skin are carried by the sensory branch of the pudendal nerve and proximal and distal perineal nerves (McKenna and Nadelhaft, 1986; Pacheco *et al*., 1997; Pastelin *et al*., 2008). Somatic afferents from the urogenital tract enter the spinal cord via L6-S1 dorsal roots (Nadelhaft and Booth, 1984). Disruption of this pathway suppressed induced ejaculation (Clement *et al*., 2006). The efferent pathways of the ejaculatory reflexes controlling the tone of the smooth muscle are conveyed by hypogastric nerves and sympathetic fibers arising from the lumbar paravertebral sympathetic chain (Nadelhaft and McKenna, 1987; Clement *et al*., 2006). The sympathetic preganglionic neurons are located in the intermediolateral cell column and the dorsal central autonomic nucleus of the lower thoracic and upper lumbar segments (T13-L2) (Nadelhaft and McKenna, 1987). The posganglionic neurons seem to be located in the major pelvic ganglia, the accessory ganglia and the pelvic plexus (Keast, 2006; Pastelin et al., 2011). The motoneurons of the external urethral sphincter, ischiocavernosus and bulbocavernosus muscles are located in the dorsomedial and dorsolateral nuclei in L6-S1 spinal segments (Marson, 1997; McKenna and Nadelhaft, 1986).

The peripheral and central signals are integrated into the ejaculation center of the spinal cord, referred to as the ejaculation generator or ejaculation spinal pacemaker (Sachs and Garinello, 1979). This integration allows for a normal ejaculatory reflex as coordinated signals sequentially relayed to the muscles and to structures of the pelvic and perineum enabling them to function in an orchestrated fashion. Because ejaculation can be observed in men and rats with high spinal transection, it has been suggested that the neurons of the ejaculation generator are located in the spinal cord (McKenna *et al*., 1991). Accordingly, tracing studies suggest that neurons of the spinal ejaculation generator are located in the dorsal gray commissure and lamina X at the L3-S1 (neurons labeled after injecting the prostate) and L5-L6 (neurons labeled after injecting the bulbocavernosus muscle) spinal levels (Marson and Carson, 1999; Tang *et al*., 1999).

Another group of neurons clearly related to the control of ejaculation has been identified in the central gray of lumbar levels at L3-4, in lamina X and in the medial portion of lamina VII (Truitt and Coolen, 2002). These cells are referred to as lumbar spinothalamic cells (LSt) and are supposed to control ejaculation (Truitt *et al*., 2003). Lesion of these neurons disrupts the ejaculatory behavior demonstrating that LSt cells are specific components of the ejaculation generator (Truitt and Coolen, 2002).

The spinal ejaculation generator is under excitatory and inhibitory influence of supraspinal sites (Allard *et al*., 2005). Indeed, stimulation of the hypothalamic medial preoptic area and paraventricular nucleus facilitates ejaculation while the nucleus *paragigantocellularis* of the medulla in the brain stem exerts a powerful inhibitory influence (Marson *et al*., 1992; Marson and McKenna, 1994). A relay center between the hypothalamus and the ejaculation seems to be located at the periaqueductal gray because lesions of this area block the reflex induced by the stimulation of the medial preoptic area (Marson, 2004).

Finally, the ejaculatory reflex is predominantly controlled by a complex interplay between central serotonergic and dopaminergic neurons with a secondary involvement of cholinergic, adrenergic, nitrergic, oxytocinergic and GABAergic neurons (Giuliano and Clement, 2005).

## THE ECOLOGY OF EJACULATION: EVERYTHING MAKES SENSE

After finishing reading the preceding sections, the reader may find him/herself wondering on how comes that a few seconds of ultimate pleasure can be so important to define each male's reproductive success. To understand this essential aspect of ejaculation, we must take in consideration the cost of gamete production. Although conventional wisdom suggests that the metabolic cost of producing spermatozoa is relatively low, recent evidence showing increased longevity following impaired gamete production argues otherwise. In addition, the fact that mating and courtship also are associated with reduced lifespan further support that wasteful sperm expenditure is costly for males (Fisher *et al.,* 2006). Hence, males must devise sexual and reproductive strategies aimed at using prudently their reproductive resources, thus reducing the cost the semen wasting.

## Ecological control: Sperm competition and prudent sperm allocation

For a male to use their reproductive resources cautiously, he must judge a variety of ecological factors that may provide vital information on his possibility of achieving successful paternity. The physical attributes of the female, the likeliness of a female to be a good mother and the magnitude of promiscuity of the female he is pursuing are just few examples of such factors. Predictions on the environmental elements such as food availability and climatic contingencies must also be foreseeing, since a drastic change of them may jeopardize the survival of offspring and, therefore, the long term male's inclusive fitness.

By far the best studied influence of a given ecological process on ejaculatory behavior is a phenomenon called intra-sexual competition. It is long known that sexually mature males confront each other in contests that provide to them with opportunities for displaying their physical attributes. Males that prevail over their opponents are supposed to increase their chances to be chosen by females to sire their offspring (a condition that not always occurs; Jennions and Petrie, 2000). Male rivalry, however, does not stay at the organismal level. In many mammalian species, intra-sexual competition is extended to the cellular level through promiscuity. Indeed, the majority of sexually active females copulate sequentially with more than a single male during her fertile period, a circumstance that promotes sperm competition within their genital tract (Pizzari *et al*., 2008; Parker and Pizzari, 2010). The ultimate prize of this competition is the possibility for the males' gametes to fertilize the female's egg (s). Taking in consideration this scenario, the reproductive outcome for each competing male would depend, in part, upon the number and mobility of the spermatozoa ejaculated by him relative to those inseminated by his competitors (Stockley, 2004; Pizzari *et al*., 2008). It is precisely under this scenario where the possibility of wasting the male's reproductive resources is greater if competition is not assessed adequately.

Males have evolved different strategies to reduce semen wasting while seeking improving their chances of achieving paternity. Some of these strategies involve behaviors different from ejaculation (*e.g.*, male's guarding the inseminated females after copulation). However, others strategies involve more directly ejaculation. Indeed, for some males it appears sufficient to inseminate repeatedly a single female during her reproductive period; a circumstance that presumably ensures having the female's genital tract plenty of his sperm by the ovulation time (Gomendio *et al*., 2006). Other males, however, do not avoid confrontation and they seem to participate openly and happily in sperm competition contests. These last males, however, have evolved a sperm saving ejaculatory strategy called prudent sperm allocation. In this case, males estimate the magnitude of intra-sexual competition or the levels of the female's promiscuity thus adjusting not only the amount and quality of the semen ejaculated but also their sexual reproductive behavior (Gomendio *et al*., 2006; Engqvist and Reinhold, 2007). Therefore, if sexual/sperm competition or the risk of it is high, the amount and quality of the semen ejaculated are reduced. Copulatory behavior matches this response. Indeed if the competitive context is high, the number of mounts and intromissions, as well as the ejaculatory latency, tend to decrease or are diminished significantly (Figure 1).

Another ecological aspect that deeply influences ejaculatory behavior is social rank. Indeed, ejaculatory latency is commonly shorter in subordinated than in dominant males. Although the reasons for this phenotypic difference are unclear, it is likely that in some instances it may reflect intrinsic phenotypic distinctions. This possibility is supported by observations showing a relationship between copulatory abilities, penile sensitivity and the levels of aromatase activity and testosterone/estrogen receptors expression in the brain of male rats (Olivier *et al*., 2006). Short ejaculatory latencies displayed by subordinated males could also illustrate a behavioral adaptation associated with sneaking-based reproductive tactics. This copulatory strategy is frequently observed in subordinated males since they commonly are younger, with smaller body sizes, poorer sexual experience, less favored by females and constantly threatened by their dominant competitors. So they must take advantage when the opportunity to copulate is given. The hypothesis that a short ejaculatory latency is a behavioral adaptation is supported by the fact that the values of the testes/body size index are regularly higher in subordinated than in dominant males (Preston *et al*., 2001; Holt and Van Look, 2004), and by observations showing that subordinated males, if provided with the chance of changing their social status to a higher order rank, shift their reproductive tactic from the sneaking-based to a dominance-based copulatory pattern (Rudolfsen *et al*., 2006); the latter pattern being characterized by longer ejaculation latencies and increased numbers of mounts and intromissions that could last for over 30 minutes at least in rodents.

Ejaculation also plays a major role in enhancing male's self-sexual assertion, sexual sociability and reproductive success in various mammalian species. In male rodents, for instance, ejaculation (and probably the pleasurable orgasmic perception commonly associated with it) is the most reinforcing component of sexual behavior and induces a reward after copulatory encounters (Phillips-Farfán and Fernádez-Guasti, 2009; Tenk *et al*., 2009). Interestingly, ejaculation-related sexual rewarding increases the availability of androgen metabolites in the male's urine. The urinary presence of these metabolites indicates that males are sexually experienced, a fact that makes them preferable to females searching for a reproductive partner. Finally, masturbation as an expression of ejaculatory behavior permits males to enhance their sexual behavioral responses, to reduce anxiety levels and to renew sperm stores in preparation to forthcoming sexual encounters; this makes masturbatory behavior an adaptive process. Although masturbation has long thought to be essentially a human, recent experimental data support that masturbatory activity also occurs in other primates (Hull *et al*., 2006).

In sum, from an ecological perspective ejaculation is much more than a physiological process involved in male-to-female sperm transfer. It allows the male to preserve their reproductive resources, to socialize his sexual/reproductive behavior, to publish their sexual abilities, to gain sexual self-confidence and ultimately to increase his chances of being a father. This might explain why male bodies have gone far to develop an intricate system to control ejaculation and why altered ejaculation could be so disturbing, as it will be discussed.

## THE EJACULATE: A *sui generis* FLUID

The semen expelled during ejaculation is also known as seminal fluid. It is typically translucent with a white, grey or even yellowish tint. The amount of semen ejaculated varies noteworthy among mammals (*e.g.* 1 ml in rams; 3 ml in men; 9 ml in dogs; 70 ml in stallions and 250 ml in boars). The human ejaculate clots and then lyses, whereas in many rodents a seminal plug is formed following ejaculation (Luke and Coffey, 1994).

The ejaculate is constituted by cells, the spermatozoa and by fluid called seminal plasma. The seminal plasma results from the mixture of secretions from the male accessory sexual glands. Among mammals, no other organs present such an anatomical and biochemical diversity as these accessory structures. Indeed, while rats display seminal vesicles, prostate, coagulating and bulbourethral glands, dogs only have the prostate. Seminal vesicles are absent in carnivores and are well developed in man, stallion, rat and guinea pig. Three distinct anatomical and histological lobes (dorsal, ventral and lateral) with different functions characterize the prostate in rats, whereas in dog and man, the prostate appears as a single structure. A pair of bulbourethral glands are present in most terrestrial mammals but are absent in the aquatic ones, and there are three pairs in some marsupials (Rodger and Huges, 1973). Such an impressive variation might reflect the vast diversity of environments and reproductive habitats in which mammals live (Luke and Coffey, 1994).

### The semen and seminal plug

The average volume of the human ejaculate is 3 ml (ranging from 2 to 6 ml). The spermatozoa are present in the range of 100 million/ml and constitutes less than 1 % of the total volume of the ejaculate. The major volumetric contribution of the ejaculate comes from the seminal plasma of which the seminal vesicles allot 1.5 to 2 ml, the prostate 0.5 ml, and bulbourethral glands 0.1 to 0.2 ml. The seminal plasma provides a nutritive and protective medium for the spermatozoa during their deposition into the females' reproductive tract. The importance of male accessory sexual glands is highlighted whenever they become dysfunctional.

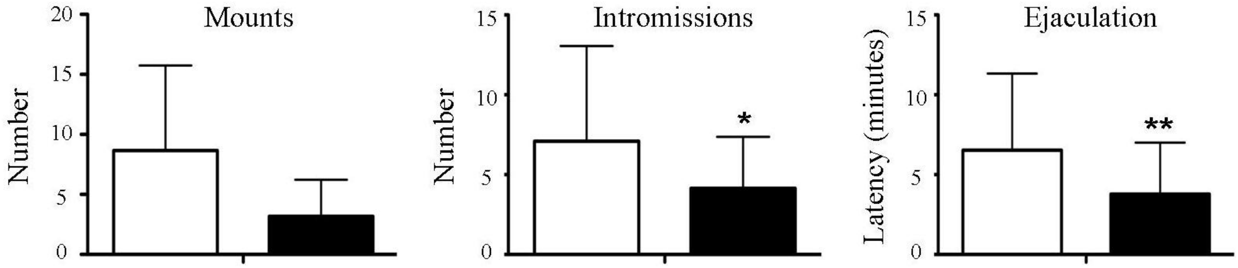

Figure 1. Male copulatory behavior under two different contexts. Non-competitive (open bar) and intra-sexual competition (closed bar). Mann-Whitney Rank Sum Test *$P$<0.015, **$P$=0.048

The mammalian spermatozoon has two main components, the head and the flagellum (or tail), which are bridged by the neck. The head contains the nucleus and acrosome surrounded by cytoskeletal components and cytoplasm. The sperm nucleus contains have of the genetic material including one or the other of the sex chromosomes (called X or Y); chromatin in the spermatozoids nucleus is highly condensed. The flagellum contains a central axonema surrounded by an outer dense fiber. In the anterior flagellum there are mitochondria forming in a tight helix around the dense outer fibers (Eddy and O´Brien, 1994). Although all mammalian spermatozoa have these general characteristics, there are species-specific differences in the size and shape of the head and length and relative size of the flagellum.

When mammalian sperm are released from the seminiferous epithelium, they are immature and acquire forward motility and the ability to fertilize eggs as they pass through the epididymis, where they undergo substantial changes in function, composition and organization, the pattern and effectiveness of flagellar activity and the ability to bind to the zona *pellucida* (Orgebin-Crist and Fournier-Delpech, 1982; Robaire and Hermo, 1988). Changes in plasma membrane composition and organization contribute to functional modifications, and involve changes in surface charge, lipid composition, protein composition and antibody binding (Eddy and O´Brien, 1994).

The fluid portion of the ejaculate is the seminal plasma. Its components vary across mammalian species (for a review Poiani, 2006; also Table 1). Poani (2006) has recently revised the role of the seminal plasma in sperm capacitation, sperm competition and fertilization. Sperm capacitation is any modification undertaken by spermatozoa facilitating them to become capable of achieving successful fertilization. Capacitation, on the other hand, is process that involves the acquisition of a coat of carbohydrates that form the glucocalyx. This is necessary for the accomplishment of full capacitation and fertilizing ability.

This is important since the outcome of sperm competition (see below) and sperm viability is affected by spermatozoa speed and mobility (Birkhead *et al.*, 1999) considering the female reproductive tract represents as a particularly hostile environment (Poiani, 2002). Seminal plasma could have allospermicidal function, so the sperm of a competitor male could be eliminated by a chemical attack (Poiani, 2006). In fact, seminal plasma of healthy men may contain cytokines that potentially could damage the sperm of others. In addition, contains leucocytes that not only could attack competitor sperm but also to remove defective sperm (Tomlison *et al.*, 1992).

Table 1. Seminal plasma components in different species.

| **Seminal plasma constituents** | **Function** |
|---|---|
| *Cells* | |
| macrophages, monocytes and polimorphonuclear leucocytes | Produce immune reaction against foreign bodies (man) |
| *Peptides* | |
| spermadhesins | Sperm capacitation (boar) |
| calcitonin and carnitine | Sperm motility (man) |
| semenogelin | Seminal fluid coagulation (man) |
| semenoclotin | Copulatory plug formation (mouse) |
| phospholipases | Sperm motility (bull) |
| phospholipase | Acrosome reaction (bull) |
| vitronectin | Acromose reaction (man) |
| *Poliamines* | |
| putrescine | Seminal clot formation (man) |
| spermidine and spermine | Seminal clot formation (rat) |
| *Catecholamines* | |
| adrenaline and noradrenaline | Modulate immune activity in the female reproductive tract (man) |
| *Eicosanoids* | |
| prostaglandin | Sperm defense (man) |
| *Alkaloids* | |
| beta-endorphin | Sperm defense (man)<br>Reduce female mating receptivity (rat) |
| *Salts* | |
| bicarbonate | Sperm motility through control of pH (man) |
| urate | Protect spermatozoa against oxidative damage in female reproductive tract (man) |
| *Metals* | |
| zinc | Inhibit lymphocyte proliferation in female reproductive tract (man) |

In humans, it is unresolved why the seminal plasma presents coagulation and liquefaction. However, it is known that infertile men may have impairment of the liquefaction process. The coagulation and liquefaction of semen vary in different species, *e.g.* the semen of bulls or dogs do not coagulate, while semen of rats and guinea pigs ejaculate a firm pellet that does not liquefy. Human semen coagulates within 5 minutes after ejaculation into a semi-solid gel and upon further standing for 5-20 minutes the clot spontaneously liquefies to form a viscous liquid (Tauber *et al.,* 1975).

In mammals, seminal vesicles secretions are involve in coagulation and prostatic enzymes in the liquefaction. The proteins secreted by the seminal vesicles are major proteins and enzymes involved in the rapid clotting of the ejaculate. In man, the major clotting protein has been termed semenogelin, and it serves as a substrate for prostate-specific enzymes that degrades the clot (Aumuller *et al.,* 1990). It is unknown why clotting and lysing mechanism is important to the reproductive process.

Seminal plugs are found in some mammalian species particularly in those in which females copulate with different partners. Because multi-partners mating results in sperm competition among males, the evolution of certain biochemical mechanisms enhances seminal coagulation to copulatory plug formation (Dixson and Anderson, 2002). The function of the copulatory plug is to prevent back-flow of semen and/or to interfere with the ejaculates of other males. The existence of a hard plug, which completely fills the lumen of the vagina of certain mammals, has been known for more than one hundred and fifty years. Many studies exploring the role of the seminal plug have been done in rats. Copulation in rats includes 10 to 15 intromissions culminating in ejaculation. Upon ejaculation sperm are expelled first, followed by secretions from the accessory sexual glands that harden into the vagina to form the seminal plug. This plug adheres to the cervix and vaginal walls, and it is necessary for sperm transport (Blandau, 1945).

Primates, rodents and artiodactyls present the seminal plugs. Among primates, chimpanzees and orangutans present seminal plugs but are absent in gorillas and humans. This may be due to the relative lack of male-male competition during mating of gorillas and humans. Among rodents, guinea pigs, rats, hamsters, and mice present seminal plug after ejaculation. Until now, among artiodactyls, the domestic pigs have a copulatory plug after copulation.

In general, it was recognized that sexual selection might continue after insemination, and that rather than competing for partners, males compete for fertilizations. The presence of a seminal plug is one of the reproductive strategies to increase the male´s possibilities to obtain more offspring.

In rats, the hardness of the seminal plug depends on the secretions of the coagulating glands. This secretion contains an enzyme called vesiculasa that coagulate the ejaculate. When coagulating glands are totally removed, no seminal plug is formed after coitus, and sperm transport to the uterus did not occur, therefore, males were completely sterile (Carballada and Esponda, 1992). The secretions of the prostate allow the adhesion of the seminal plug to the vagina (Tlachi-López *et al.,* 2011). The weight and size of the seminal plug depends mainly on the secretions of the seminal vesicles (Carballada and Esponda, 1992). The rostral end of the seminal plug forms a cup at the vaginal cervical junction holding the sperm under pressure until transcervical transport is completed. Seminal plugs are usually loosened by subsequent intromissions by the same of different male. If plugs are dislodged in less than 6 minutes after an ejaculation, the sperm transport is disrupted (Mathews and Adler, 1977). The length of time corresponds to the male rat´s postejaculatory interval. This interval prevents the male from reassume mating, and then allows complete sperm transport in the female genital tract. However, a different male has the ability to dislodge the plug reducing or avoiding the amount of sperm delivered by the previous male, and deposit his own sperm and plug (Wallach and Hart, 1983).

## Sperm transport in the male and female reproductive tracts

Sperm transport occurs not only into the female genital tract after copulation, but also in the male genital tract after spermatogenesis. Sperm is transported passively from the seminiferous tubules to the *rete testis*, and then to the efferent ducts. These ducts become highly convoluted as they reach the epididymis, which is a single, long and highly convoluted duct on the posterior border of the testis. The epididymis is divided in caput, corpus and cauda. Peristaltic movements of the epididymis propel the spermatozoa from the caput to the cauda. Transit through epididymis is slow and constant in several species (Harper, 1994).

Therefore, during seminal emission the mature spermatozoa from the epididymis cauda are transported through the vas deferens and proximal urethra and then are mixed wiith the secretions of the accessory sexual glands. Then the ejaculate (seminal plasma and sperm) is expelled by the urethral *meatus.*

Most male mammals deposit their ejaculates into the vagina. The pH of the vagina is acid; this acidity is maintained by the presence of lactic acid due to the action of *Doederlein bacilli* on the vaginal secretions. Seminal plasma serves as a buffer protecting sperm. The vagina is a hostile environment to spermatozoa and those that are not rapidly entrapped in the cervical mucus die and are voided to the exterior (Fox *et al.,* 1973).

In primates, immediately after ejaculation, seminal plasma coagulates; the coagulum is broken down by proteolitic enzymes. In one hour, the material is liquefied and spermatozoa are motile. The coagulum probably acts to retain spermatozoa in the vagina close to the cervix, thus permitting maximal access for the spermatozoa to become entrapped in the cervical mucus. During coitus, intravaginal pressure is negative but becomes positive during female orgasm. Then it is possible that, the vaginal pressure and the smooth muscle vaginal activity will also propel the spermatozoa into the cervix (Harper, 1994). The consistency, of cervical mucus forms the basis for the ovulation method (Billings) of naturally family control (Billings *et al.,* 1972).

The women cervix has crypts; it seems that only motile spermatozoa are lodged in these crypts. It has been suggested that the cervical crypts serve as reservoirs allowing a continued release of viable spermatozoa approximately during hours (Harper, 1994). The filtering action of the cervical mucus is a mechanism to guarantee that only the fittest spermatozoa ascend toward the site of fertilization. Cervical mucus from infertile women contains cytotoxic antibodies to their partner´s spermatozoa inhibiting sperm motility (Marthur *et al.,* 1988). Even though the cervix represents a major barrier to sperm ascent, many spermatozoa reach the uterus. In contrast, in those mammals which ejaculates are deposited in the uterus, *e.g.* pigs, a great quantity of sperm is found in uterus (Harper, 1994). Nevertheless, the uterotubal junction constitutes a barrier to sperm ascent. The uterotubal junction is between the uterus and the oviduct. During transit into the female tract, sperm undergo the so-called capacitation, and is required for fertilization. This consists of a destabilization of the plasma membrane of sperm head without any visible morphological changes.

In a few words sperm transport depends on several factors, not only of flagellar movement. In the male tract depends on seminal plasma, the contraction of the reproductive ducts and muscles of the perineum. This allows the expulsion of semen through the urethra. Once deposited the semen in the female, sperm transport depends on the pressure of the seminal plug (if applicable), changes of the intravaginal pressure and activity of the oviduct to reach the site of fertilization.

## DISORDERS OF EJACULATION: FALLING HOPES WITH ADAPTIVE VALUE?

Until a few years ago, the human medical community considered ejaculatory disorders as having a purely psychological etiology. Fortunately, this concept changed over the past decade or so, springing the elaboration of a wealth of studies aimed at characterizing the psychological and organic factors that lead to "ejaculatory disorders" in human and non-human mammalian species (*e.g.,* rats, mice and horses) (human and rats, Waldinger, 2002; horses, McDonnell, 1992). As a result, it is now recognized that ejaculation is normally preceded by semen emission and followed by an orgasmic perception in mammalian males (Newman *et al.,* 1991). We also are now aware that when each or all of these phases "malfunction", males develop sexual symptoms that have relevant reproductive consequences.

### Precocious ejaculation, anorgasmia, delayed ejaculation and retro-ejaculation

A classification of ejaculatory disorders has also emerged as a result of these investigations. Emission phase disorders are so far exemplified by retrograde ejaculation. Ejaculation phase disorders conjunct premature, deficient/partial and delayed ejaculation, anejaculation, azoospermic ejaculation and urinary incontinence. Orgasmic disorders include anorgasmia and the so called postorgasmic illness syndrome (Jannini and Lenzi, 2005). Even though all these conditions may be conceived as disorders and in many cases could be associated with abnormal conditions, at least some of them might also reflect physiological strategies to cope with sexual competition and/or promiscuity and may have psychogenic and organic components (Lawrence, 1984; McDonnell, 1992). In the following paragraphs we will speculate on this possibility by commenting on cases and ecological scenarios where a presumed ejaculatory dysfunction could have an adaptive value.

We will begin by considering premature ejaculation. Main stream urologists, sexologists and human reproductive biologists would probably coincide that premature ejaculation is undoubtedly the most frequent ejaculatory problem encounter in their medical practice (Jannini and Lenzi, 2005)) Nevertheless, as mentioned before, short ejaculatory latencies are characteristic of subordinated males. In natural settings, this behavioral feature exemplifies a reproductive strategy that allows males to increase their chances of having copulatory encounters avoiding the physical confrontation with dominant males and the possibility of being harmed (Lawrence, 1984). Also ejaculating faster would increase the males' opportunities to copulate with more females. In this context, prematurely ejaculating males could well represent an endo-phenotype that can be modified by sexual training or by changing social status, but it is never considered as an abnormal condition. Thus, human males "suffering" of premature ejaculation might only represent a phenotypic variety associated with "unconscious" subordination. The observation that premature ejaculation is diagnosed to a similar percentage (25 %) among male human populations around the world regardless of credence and of economical or social status (Jannini and Lenzi, 2005), lends support to this notion.

Human delayed ejaculation is also considered as an ejaculatory malfunction (Jannini and Lenzi, 2005). In male rodents, however, delayed ejaculation has an adaptive value since female rats require long-lasting stimulation to reach the sexual excitement needed to increase their chances of getting pregnant (Toner and Adler, 1986). This may explain why dominant male rats in the wild have developed a copulatory strategy that enables them to delay their ejaculation for approximately 30 minutes while providing adequate female sexual stimulation; if males succeed their inclusive fitness may increase (Pattij *et al*., 2005). Once again, delayed ejaculation in humans may only reflect a phenotypic variation related with reproductive strategies that could increases their possibilities of fathering offspring, and do not necessarily reflect a dysfunctional state.

Mammalian males may show no ejaculation or produce azoospermic ejaculates in spite of displaying normal sexual arousal and persistent mounting and thrusting. Although at first glance both circumstances might seem abnormal and non-sense since males would decrease their inclusive fitness, self-assurance and sexual interest while increasing their frustration and aggressiveness (McDonnell, 1992), anejaculation and azoospermic ejaculation could also have an adaptive value in natural, ecologically meaningful settings. In particular, if males are confronted with copulatory contexts of relatively high intra-sexual competition, they may choose during copulation to remove the semen of their competitors that copulated before with the female (Ramm *et al*., 2005) while saving their own sperm stores for better opportunities. Even though under this scenario males would not win the competition, they would certainly impair the reproductive success of their competitor males. A similar case might be casted for deficient or partial ejaculation since it could very well be the result of physiological mechanisms modulating differential sperm allocation under high pressures associated with sperm competition.

The last example of “ejaculatory dysfunctional states” that might have an adaptive value when evaluated in natural setting is the so called anorgasmia (Jannini and Lenzi, 2005). How can anorgasmia be adaptive at all for males? Ejaculation and orgasm are known to reinforce the couple´s bonding strength (Nelson and Purdon, 2011). This, however, is opposite to the reproductive interests of males whose instincts are known to drive them to look after more than a single female to fathering offspring. Clearly, if males avoid the reinforcing effects of ejaculation and orgasm through anorgasmia, they could pursue more easily their reproductive interests by creating lose bonds with their reproductive female partners. In many cases such “dysfunctional states” might only be distinct functional traits that clearly reflect the variability and plasticity of the mammalian sexual phenotype. Unfortunately, biological evolution is not driven by social precepts and does not necessarily match social needs.

## CONCLUDING REMARKS

Ejaculation constitutes a fundamental process in the males’ reproduction. The process requires efficient propulsion system to ensure semen transport through the male urethra and its expulsion into the vaginocervical tract. In spite of one spermatozoon is required to fertilize an ovum, millions of them are expelled, presumable due to sperm competition. Great efforts have been made by mammalian males to evolve intricate mechanisms essentially designed to avoid wasteful use of semen (e.g., prudent sperm allocation). Although it is conventionally believed that males are always ready to copulate and ejaculate, the evidence discuss support that neuroendocrine mechanisms exert powerful inhibitory actions that must be overcome by the male to achieve ejaculation. And even then, subtle mechanisms as yet poorly understood prevent males to make unrestrictive use of their costly reproductive resources under unfavorable copulatory contexts. The existence of different male copulatory phenotypes, even those considered as ejaculatory disturbances in humans, may be considered as reproductive strategies evolved through evolution.

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