

A Sex Cycle in the Male¹

Menstruation is unique among the normal physiological processes in that it involves a waste of blood. Since early in the history of mankind this easily observed and regularly recurring phenomenon has been the subject of speculations about the cyclic nature of the female sexual functions. In popular belief the human menstrual cycle has a length of a lunar month (mensis, Lat. a month). The abundant occurrence of mythical and religious ideas about the origin and background of menstrual bleeding reflects the popular interest in this process. However, only in primates does the female sexual cycle involve regular bleedings. In other mammals this periodicity is even more striking, the sexual receptivity of the females being restricted to heat periods. The sexual functions of the females thus obey an all-or-nothing law.

In many mammalian species the reproductive functions are performed only during a limited breeding season. During each of such seasons non-pregnant female animals show one or several heat periods. The males on the other hand are usually ready to mate at any time during a breeding season. Consequently the variation of the male sexual functions must be purely quantitative and more difficult to observe. In man the conditions are most complicated by the many psychological factors influencing human sexual activity. Therefore, to begin with animals are more suitable for investigating, whether or not rhythmical phenomena occur also in the sexual functions of males. In animals which can be brought to ejaculate into an artificial vagina, e.g. rabbits and cattle, the seminal volumes and the amount of yielded sperm cells are quantities suitable for study in such an investigation. However, the volume as well as the composition of the ejaculates are influenced by such factors as food supply, light conditions, frequency of ejaculation, etc. Therefore, a cyclic variation in these quantities, if existing, can appear only under strictly standardized conditions.

The earliest report on cyclic phenomena in the 'fecundity' of males was published in 1956 by VIRGINIA DOGGETT² and dealt with the variation of the number of sperm cells in daily yielded ejaculates from rabbits. Independent of her report, KIHLSSTRÖM³ observed a similar periodicity in the volumes of the ejaculates under the same conditions. These observations have since been extended to other sexual functions of the rabbit as well as to other species⁴⁻²⁰.

When collecting semen from rabbits once a day, ejaculates occasionally occur which by their large volume markedly deviate from those of other ejaculates (Figure 1). This happens more or less regularly with an interval of about 5 days. A statistical treatment of the data collected in this way reveals a significant cyclic variation⁴. In bulls there is a similar periodicity in the volumes of the yielded ejaculates^{6,8,20}. In this species, however, the length of the period is of quite another magnitude, viz. about 4 weeks. The volumes measured include the sperm cells, but are quantitatively dominated by the fluid from the accessory glands, especially in rabbits, where the sperm cells constitute only a small part of the ejaculate. The gelatinous substance sometimes occurring in rabbit semen appears cyclically with the same periodicity⁷, and also the secretion of fructose by the accessory glands varies rhythmically in the same manner¹⁷. It is thus evident that the secretory activity of these glands is submitted to a periodical variation.

When collecting semen regularly, a cyclic variation in the amounts of sperm cells per ejaculate has been found in rabbits², bulls^{6,8,20}, and men⁵. The epididymis and the

vasa deferentia contain a considerable store of sperm cells which cannot be discharged by a few ejaculations. Therefore, the periodicity found is not dependent upon a rhythmically varying production of sperm cells in the testis. Most probably the efficiency of the mechanism transporting spermatozoa through the genital ducts is subjected to a cyclic variation. The cyclically varying properties of the same individual are more or less synchronous. Thus correlations between amount of sperm cells on the one side and motility, seminal volume, and amount of the gel on the other have been demonstrated in rabbits².

It might be suspected that the regular provocation of the animals to ejaculate into an artificial vagina influences the results obtained. However, as isolated male rats deliver ejaculates spontaneously without external stimulation²¹, these animals are suitable for an investigation of the endogenously regulated variations in the seminal characteristics. The semen yielded coagulates at the ejaculations which appear to be plugs, having a consistency similar to that of India rubber. Under ordinary conditions these plugs are eaten by the animals. By preventing the animals from grooming their penis orally, by means of a girdle, made from plaster of Paris, around their chests, it is possible to collect these ejaculates. In this way it has been demonstrated that in the rat the amount of semen yielded at the spontaneous ejaculations varies cyclically¹⁶.

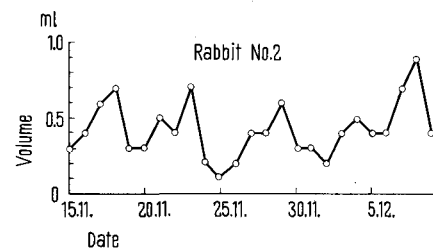


Fig. 1. Variation in the volumes of daily ejaculates from a rabbit.

- ¹ For valuable discussions and advice I am obliged to Professor P. E. LINDAHL.
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- ³ J. E. KIHLSSTRÖM, *Studies on some Activities of the Male Accessory Glands, Especially the Production of Male Sperm Antagglutin and their Relations to Fertility* (Uppsala 1958).
- ⁴ G. DEGERMAN and J. E. KIHLSSTRÖM, *Acta physiol. scand.* 51, 108 (1961).
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Whether or not fertility varies in the same manner is a question of great theoretical and practical interest and can be studied in bulls used for artificial insemination. One single ejaculate from such a bull may under optimal conditions be distributed among more than 100 cows. KIHLSSTRÖM^{6,8} and KIHLSSTRÖM and HULTNÄS²⁰ found fertility, determined as the number of pregnancies in % of the number of inseminations performed, to vary cyclically with a mean difference between maxima and minima of 19%, the highest value found in one bull being 43% (Figure 2). There seems to be a difference in phase between this cyclic variation in fertility and the cycles observed in the volumes of the ejaculates and their amount of sperm cells. Thus the variations of seminal volume and the amount of sperm cells per ejaculate are significantly correlated to changes in fertility occurring some days later²⁰.

In many species the oestrous cycle of the females includes also a cyclic variation in body temperature. In male rabbits a similar periodicity has been found (Figure 3)⁹. Moreover, to a certain degree, changes in seminal volume and body temperature take place simultaneously⁹. Attempts to demonstrate a cyclic variation in the body temperature of men, male rats, and guinea-pigs have not been successful¹⁸.

A study of the cells exfoliated from the vaginal mucous membrane clearly reveals the phase of the oestrous cycle. It is also known that the frequency of non-keratinized cells in the male urethra in men as well as in rabbits increases after treatment with oestrogens and after castration, but decreases after treatment with testosterone²²⁻²⁴. Starting from these facts, KIHLSSTRÖM and HORNSTEIN have studied the daily exfoliation of cells from the male urethra in rabbits¹⁰⁻¹². They characterized 5 different types of cells: 1 completely cornified and 4 types representing different stages of beginning cornification. All types of cells except the first-mentioned occurred with cyclically varying frequencies. Consequently also the exfoliation of cells from the mucous membrane of the urethra is subjected to a cyclic variation. Besides, a rise in the seminal volume often runs parallel to an increase in the frequency of the cells which are in an early stage of cornification. Recently a cyclic variation in the exfoliation of cells from the male urethra has been demonstrated in men as well¹⁹. In the light of the hormonal influence upon the frequency of non-keratinized cells, these observations strongly indicate a hormonal regulation of the male sexual cycle.

As in female animals, it might be expected that also in males the cyclic variation of the sexual functions influences the sexual behaviour. When collecting semen from rabbits by means of an artificial vagina, DEGERMAN and KIHLSSTRÖM⁴ found the time elapsing from the presentation of the dummy until the buck began with pelvic thrusts to vary cyclically with the same length of the period as found in other properties (Figure 4). This time might be regarded as an inverted expression of the strength of the sexual drive. Apparently also the sexual behaviour of the bucks is subjected to a rhythmical variation.

The periodicity changes with the age of the animals. The cycles are longer in puberal rabbits than in mature ones, and with growing age approach the shorter duration found in adult animals². In bulls the regularity of the rhythmicity in fertility decreases with increasing age^{6,8}.

The factors regulating the periodicities may be external or internal. As to the variation in the seminal volume it is possible that an unusually big ejaculate is followed by a markedly long interval before the sexual glands have

produced enough secretions to yield another big ejaculate. This being the case there should be a positive correlation between the maximum volumes and the intervals following up to the next maximum volume. However, there is no such correlation⁴.

The environment does not influence the cyclicality, as neither maxima nor minima coincide among animals caged in the same room and treated in the same way^{2,9}. Not even the presence of female animals influences the cycles of the males⁹. Besides, it might be suspected that the regular collections of semen induce a periodicity, but the length of the cycle is not influenced by changing this frequency²⁰. Neither is the period length altered by collecting more than one ejaculate per day^{2,17}, nor by giving the animals a period of rest². In this connection it must be stressed that in the rat the cyclic variation occurs in the spontaneous sexual activity¹⁵. The synchronous changes in the cyclically varying properties of the same

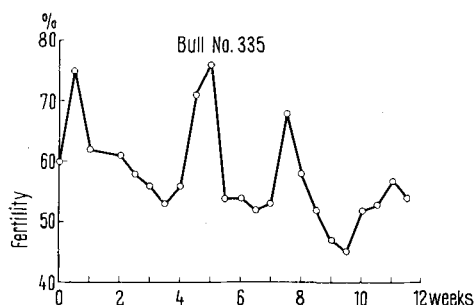


Fig. 2. Variation in the fertility of a bull during 12 successive weeks (2 ejaculates a week).

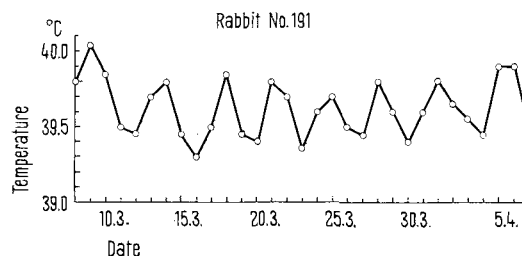


Fig. 3. Daily variation in the body temperature of a rabbit.

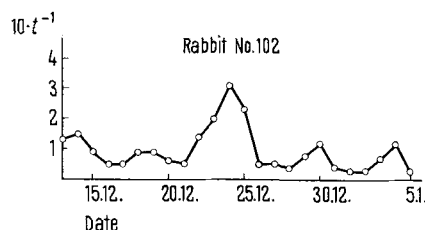


Fig. 4. Daily variation in the sexual drive of a rabbit. t = time in sec from the presentation of the artificial vagina up to the beginning of the pelvic thrusts.

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²⁴ H. G. BERTHELSSEN, *Acta Endocr.* 29, 375 (1958).

individual also point to an internal origin of the phenomena^{2,9,11,12,20}. Finally, the relationship between the age of the animals and the cyclic phenomena indicates an endogenous regulation^{2,6,8}. Consequently, an endogenous origin of the periodicity seems most probable.

The similar arrangement of interacting gonadotrophic and gonadal hormones in both sexes makes it plausible to expect a hormonal regulation of the cyclic phenomena also in males. Interest was directed towards this possibility already in the earliest communications²⁻⁴. The question has since then been studied further by KIHLSSTRÖM et al.^{7,11,12,17}. Besides, the hypothesis of a hormonal regulation of the male cycle has been supported by INOUÉ^{13,14} and MÅNSON¹⁶. The production of the gelatinous substance occurring in rabbit semen is known to be stimulated by androgens^{25,26}, and this gel appears periodically⁷. As in females, oxytocin has different actions in different phases of the cycle, indicating that also the male cycle may have a hormonal origin²⁷. Furthermore, 6-8 days after castration of rabbits the cyclic variation in exfoliation of cells from the male urethra disappears and thus depends upon testicular hormones^{10,12}. Only the frequency of the completely cornified cells, which does not vary periodically in the intact animals, remains the same also after castration. In contrast to the female animals the temperature cycle in males is independent of gonadal hormones, and persists after castration^{10,12}. In an adult man MÅNSON¹⁶ has found a 4-week cycle in the variation of the frequency of neutrophil leucocytes with androgen-induced nucleus appendages. It thus seems probable that the secretion of the testicular hormones varies cyclically.

Ovulation and luteinization occur very rarely in ovarian grafts in normal as well as in castrated males²⁸ and a vaginal epithelium near such a graft shows a continuous or prolonged cornification²⁹. These facts seem to exclude the possibility of a cyclic variation in the secretion of gonadotrophin by males. However, INOUÉ¹⁴ has assumed that the hypophysis of the normal male rat cyclically secretes gonadotrophins, and that the amounts suffice for the stimulation of ovarian grafts to secrete oestrogen acyclically, even at times when the gonadotrophin secretion is at a minimum. Taking this into account, he has tested this hypothesis by diluting the male gonadotrophins by very skilful experiments using normal males in parabiosis with castrated and hypophysectomized males bearing ovarian and vaginal grafts. By these means he has demonstrated a cyclic variation in the secretion of gonadotrophins in the male rat¹⁴.

It is of some interest to compare the length of the male sexual cycle with that of the oestrous cycle in the same species. The oestrous cycle of the female rabbit has a length of 4-6 days³⁰ which is in good agreement with that of the male cycle, viz. 5.5 days with 68% of the values falling within 5-7 days^{4,7,9,11,12}. In bulls the length of the cycle is about 4 weeks with 64% of the values falling

between 2.5 and 4.5 weeks^{6,8,20}, which nearly coincides with the length of the oestrous cycle of the cow, viz. 21 days. Also in the rat the length of the oestrous cycle and that of the male cycle is the same, viz. 4-6 days¹⁵. In men DOGGETT and KEILERS⁵ have found the amount of sperm cells and fructose in daily ejaculates to fluctuate with a period length varying from 2-5 days only. However, their material comprises 7 persons, none of them having been studied for more than 17 successive days, and possibly existing longer cycles have therefore not been observed. EXLEY and CORKER³¹ have found a cyclic period of 8-10 days for urinary oestrone and 17-oxo-steroids in human males, and this cyclicity is interpreted to be of testicular origin. Their material comprised 4 men, 1 of them having been studied for 90 consecutive days, 3 of them for 17 days. On the other hand MÅNSON¹⁶ has found a 4-week cycle in the frequency of leucocytes having androgen-induced nucleus appendages, and HORNSTEIN¹⁹ recently revealed a 4-week cycle in the exfoliation of cells from the human male urethra.

All facts so far known supply strong indications for the existence of a male sexual cycle in rats, rabbits, bulls, and men, having about the same length as the female sexual cycle of the same species. Very little is known about the regulation of the cycle, but some observations point to a hormonal dependence, similar to that of the female cycle.

Zusammenfassung. Physiologische Untersuchungen verschiedener Sexualfunktionen bei Kaninchen, Bullen und Ratten erbrachten im Verlaufe einiger Jahre Hinweise auf einen männlichen Sexualrhythmus, der gewisse Ähnlichkeiten mit dem weiblichen Östruszyklus erkennen lässt. Zyklische, quantitative Schwankungen in der Zahl der Spermien, dem Volumen des Ejakulats, der Fertilität, der sexuellen Erregbarkeit, der Körpertemperatur und der urethralen Zellexfoliation wurden nachgewiesen. Die Ergebnisse von Kastrationsversuchen sprechen für eine hormonale Steuerung dieses Zyklus. Einige Beobachtungen lassen daran denken, dass auch bei Männern ein ähnlicher Zyklus besteht.

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