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# SEASONALITY, FOLLICULOGENESIS AND LUTEOGENESIS IN MARE OVARIES

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Summary. In the horse the circannual rhythm of reproduction is cued primarily by photoperiod changes. This environmental signal is translated to an endocrine signal in the habenulo- pineal gland. In the mare, short daylenght is associated with a decrease in gonadotropin secretion and consequently a decrease in ovarian activity. The ovary of the mare is unique in its structure and different from other mammals. Ovaries were cut around the fossa ovulations, and analyzed during the seasonal period of mare (10) estrus cycle (March-July). Tissue sections were fixed in Bouien fixative, and then HE stained. The relationship of localization of cortex., medulla and fossa ovulations is investigated. The ovulation fossa is localized in the center of the ovary and is surrounded by broad ovarian cortex. Medulla is localized in a narrow peripheral area. The cortex area ahead of the fossa is occupied by developing follicles. Variously sized follicles were identified and ovocyte-cumulus connections will be considered. The inside cavity from the evacuated follicle, fills rapidly with blood forming Corpus Hemorrhagicum followed by creation of lutel tissue. Corpus Luteum in mare is the largest comparing the other animals, pear-triangle shaped, size 0.5-1 cm, covered by dense tunica albuginea, inside the fossa.

The regulatory mechanisms of seasonality are on the strong influence and connection between hypothalamo-pituitary-gonadal axis and we discuss the implications with regard to investigation strategies to advanced the onset of cyclic reproductive activity in the early spring.

Key words: Seasonality, ovary, mare, reproduction, folliculogenesis, luteogenesis

#### Introduction

Beyond doubt, horses are unique in reproductive behaviouring. A long-standing curiosity in equine reproduction science and veterinary practice concerns what appears to be lower rates of sexual vigor and fertility and higher rates of sexual behavior dysfunction among hand-bred domestic horses compared to equids breeding at liberty (1). Under the strong influence of seasonality, and consequently with delicate mechanism of regulation, they have a specific sex-cycle (Fig. 1). The horse is a seasonal polyestrous species with onset of the breeding season occurring in spring, associated with increase in daylight, temperature, and availability of food (2).

The mechanism whereby gonadotropin and presumably GnRH secretion is decreased during the anestrous period is not well understood in mares (3). The mare, as other seasonal breeders, has an endogenous circannual reproductive rhythm and the main role of seasonal clues appears to be to synchronize the endogenous rhythm to winter and summer (4).

The hypothalamo-pituitary-gonadal axis posseses the components of the regulatory mechanisms to per-

form most of its endocrine functions. Seasonal breeding in horse is governed by photoperiod. The signal requires a neuroendocrine transduction. The underlying neural mechanisms are still unexplained. Concerning photoperiod, dopamine, opioids and melatonin are possibly the best known mediators between brain and gonadal function. Dopamine pathways inhibit both GnRH and neurons which secrete opoid as part of photoperiodic control of gonadotropin release. GnRH is the neuroendocrine signal for ovulation (5). In the mare, dopamine antagonist, sulpiride, during late seasonal anestrus advances the first ovulation in the year and increases plasma FSH concentration, however, the treatment has no effect on LH secretion (6).

The mare is a unique model in respect with several characteristics of the estrus cycle., the in vivo conditions leading to follicular ovulation and ovocyte maturation that are partly different from those in other mammals: no ovulatory LH surge occurs but a progressive increaese in LH lasting many days, with a maximum concentration one day after ovulation (7). These species-specific events could involve some special local mechanisms during follicular growth and maturation.

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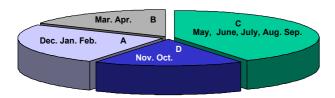


Fig 1. The seasonal reproductive cycle of the typical mare.A - Anovulatory season, B - Spring transition,C - Natural breeding, D - Fall transition

The estrous cycle of the mare averages 21 days (Fig. 2). The phases of the estrous cycle of the mare are in proestrus, for a 2 days, and estrus is 7 days. Average duration of postesrus is 2 days, following diestrus with 13-14 days, before onset of next cyclic estrus till long

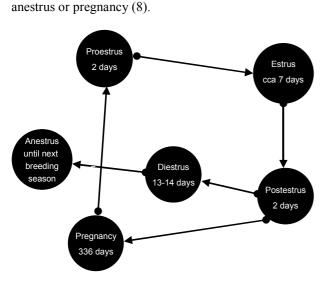


Fig 2. The ovarian cycle of the mare with alternates

Since the mare is sexually receptive for several days, it is difficult to compare some of the phases. It can be hypothesized that the long and variable length of estrus may be due to high levels of FSH followed by longer period og LH release. The serum LH curve is elevated for a week in the mare, and ovulation occurs at the peak of LH release, which in turn forecasts the end of estrus in 1-2 days in most mares (9). LH concentrations are lowest during the mid-luteal phase of estrous, rising only a few days before onset of estrus to a peak usually

on the day off, or shortly after ovulation, to then drop to previous levels over the next few days. The duration of secretion of LH in the mare and its associated ovulatory surge is considered to be longer than in most other animals (10).

FSH in contrast to LH, is believed to follow a bimodal secretion pattern, although some researchers suggest that this twin-peak effect is seen only during spring and early summer. After that, according to them, a singlepeak effect is seen during later summer and fall. In the bimodal pattern the initial FSH surge starts late in estrus and peaks early in diestrus, dropping slightly and with the second surge starting in mid-diestrus peaking in late diestrus. In the uni-modal pattern observed during the later period breeding season, researchers suggest that the initial postovulatory surge of FSH is absent. Despite measured increases in FSH it has been suggested that follicular growth itself follows a singular developmental path commencing in mid-estrus, with a mechanism that selects a single follicle for optimum growth and the subsequent ovulation. Therefore, termination of estrus is somewhat dependent on ovulation cycle.

By about 5 days after ovulation, the CL is fully functional and secreting progesterone, that is the luteal phase. Regardless of the duration of estrus, the corpus luteum is functional for a constant length of time. Therefore, most of variability in the length of the estrous cycle is due to variability in length of estrus (11). A prolonged CL is frequent factor that may influence the estrous cycle length. The luteal phase may range from 35-90 days instead of normal 14-16 d. The prolonged CL continues to secrete enough progesterone to suppress signs of estrous (12).

#### Subjects and methods

Ovaries from the 10 mares (2-10 years old) of unknown reproductive history were obtained during the breeding season (March-July) at local slaughterhouse (near Beograd, Vinca, Dragoljub Gavrilović slaughterhouse), 44.4 grades, North latitude. The mares and fillies were in good healthy condition, after the clinical examination, and after the age estimation by teeth 15 minutes after slaughter, the ovaries were measured in weight and length, and cut in the medial osse in the

Table 1. The main features of ovary

No	1	2	3	4	5	6	7	8	9	10
Age	1.5	2	2.5	3.5	4.5	5.5	7	8	10	12
S-m	May	Mar	May	Mar	Apr	Apr	May	Jun	Jul	Apr
L-o [g]	35.4	36.5	39.9	50.5	54.3	60.5	65	68.9	70	65.8
R-o [g]	25.7	29	28	32	38	40	35	38	40.6	50
L [cm]	3.5/2.5	3.5/2.5	3.8/2.5	4.5/3	5/4	5/4.5	4.8/4.5	5/4.8	5/4	4.8/3.8
R [cm]	2.5/1.5	3/2	3.2/2	3/2	4/2	4/2.8	4/2.5	3.7/3	4/3.5	4.5/4
CL	0	0	L+	L+	L+R+	L+R+	$\Gamma$ ++	L+R+	R++	L+
deG	0	0	L	L	R	0	L.R	L	0	0
cystic		L	R		L.R		L		R	R

No - mare numeration, Age - at date of slauthering, S - m - slauther month, L - o - left ovary weight in g, R - o - right ovary weight in g, L - left ovary length in cm, R - right ovary length in cm, CL - corpus luteum presence, deG - de Graffov follicle presence, cystic - cystic follicle presence

fossa ovulationes line. The ovaries were put in Bouien fixative. After 5 days in fixative tissue are prepared for staining procedure. Tissue section of 5 micrometer are prepared for Hematoxilin-eozin, AZAN and Methyl green pyronine (MGP), stained. Then, the relationship of localization of cortex, medulla and fossa ovulations is investigated. Variously sized follicles were identified and ovocyte-cumulus connections were considered. The CL position and characteristics are observed, and the presence of the CA, is notified, too.

Tissue sections are observed in Kight Microscop/ Olympus BX 41, and digital photos were made with the camera Olympus/ OLYMPUS DIGITAL CAMERA, model/ C3030Z, Normal program.

The observations are compared among the age groups, and month period from which the tissue were obtained.

#### Results

#### The main features of ovary

Ovary in mare has a kidney shape. The Left ovary is usually larger than the right one

Also, it changes throughout the aging. The main features of ovary in the oestrous cycle are represented by follicles and corpus lutea presence (Table1).

Germinal epithelium, cubical epithelial cells, is outer most layer without basement membrana, is not relevantly taller of other mammals epithelium, and belongs to fossa ovulations epithelium.

#### Fossa ovulations

The presence of an ovulation fossa is unique for horses.

This is a result of the neonatal development of the ovary, when the cortical tissue becomes confined to an area and is nearly surrounded by medullary tissue by the fourth month. Thus, there is only small area where follicles develop and ovulate- the ovulation fossa. Fossa provides path of ova to get through connective layer.

In horses cortex and medulla are reversed (Fig. 3).

#### Cortex

The cortex region is located inside the fossa o., where groups of primordial and primary folliculles can be observed, like in cohorts.

Surrounding the developing follicles is fibroblas- like cells called the ovarian stroma. These cells become theca interna cells of developing follicles or interstitial cells.

The smooth muscle fibers are very present in the cortex region where intermingle with the theca layers of developing follicles. It is though that these muscle fibers play a part in the ovulatory process.

In a small percentage the secondary follicles are noticed, compared to other species ovaries, but a lot of atretic follicle can be noticed, especially in the tertial stage (Fig. 4).

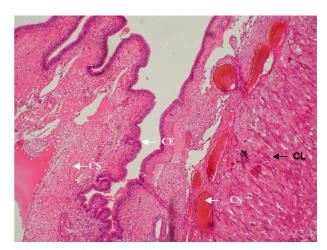


Fig. 3. The part of fossa ovulationes.

Left ovary. H-E, obj. × 10. 6 years old.

CE columnar epithelium, CS cortex stroma with vascular vessels, CL part of corpus luteum

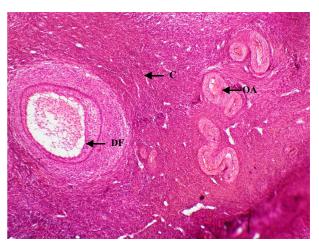


Fig. 4. The cortex region is located inside the fossa ovulationes. H - E, obj. × 10. 10 years old. DF developing follicle, C cortex, OA transitional sections of branches of ovarian arteries

#### Medulla

Outer located is area called the medulla, in mare. This area contains lymphatic tissue, nerves, blood vessels, elastic and fibrous tissue, and smooth muscle cells.

In the mare, we observed thick net of fibrous tissue. Blood vessels is very rich developed, and with aging, we can notice the signs of hialisations.

#### **Follicles**

In the cortex the grapes of primordial follicles can be observed, in cohorts (Fig. 5). The developing follicles are surrounded by fibroblast-like cell tissue called the ovarian stroma. These cells become theca interna cells of developing follicles or interstitial cells. The smooth muscle fibers, more than in other species animal, are very present in the cortex region where intermingle with the theca layers of developing follicles.

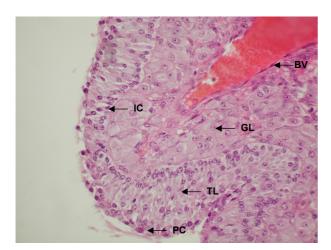


Fig. 5. The theca and granulosa cells mix of developing Corpus Luteum. H - E, obj. × 40. 3.5 years old. BV formation of blood vessels, GL granulosa luteal cells, TL theca luteal cell, IC interstitial cells, PC plasmocyte

The size of the Graafian follicle ranges from 2-10 cm. Most follicles are 3.5-5.5 cm, in diameter at the time of ovulation. Almost all Graafian follicles are tense and firm on rectal palpation within the first few days of estrum but within 16-24 hours of ovulation many follicles lose their tone and become softer and slightly fluctuating.

The mature Graafian follicle is somewhat triangular or pear-shaped with the largest portion of the follicle palpable during estrus on the convex curvature of the ovary or at either pole of the ovary. The narrow stalk – like portion of the follicle protrudes toward the concave portion of the ovary or the ovulation fossa where ovulation invariably occurs in close proximity to the rather small fimbriated portion of the uterine tube. Only rarely does ovulation occur more than 2 cm from the ovulation fossa.

Follicle can be palpated, but not the CL.

Since the mature follicle is highly vascular and the theca interna layer is hyperemic at ovulation, rupture of some vessels occur and clotting is delayed, hemorrhage occurring into the large cavity of the former follicle produces a soft, pulpy hematoma that can be palpated per rectum, as a soft, mushy depression on the greater curvature of the ovary for 24-36 hours after ovulation.

### Corpus luteum

CL formation is in response to LH surge, granulose and theca cells of preovulatory follicle luteinize. Basement membrane disintergrates. After ovulation the walls of the follicle collapse. Theca and granulose cells mix. Basement membrane becomes the connective tissue network of CL. Breakage of small blood clot seen in the corpus hemorrhagicum.

The mare has by far the largest corpora hemorrhagica of all domestic animals.

Developing CL is a carnation shaped and in a rich fold of luteal tissue a angiogenic veseels can be seen (Fig. 6).

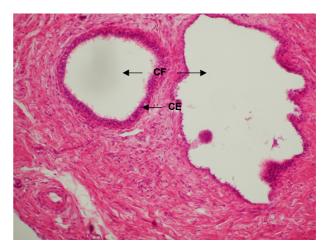


Fig. 6. Deviation in fossa cortex: Cystic formes. H - E, obj. × 20. 12 years old. CF Cystic formes, CE Pseudostratified ciliated epithelium

In the same time a fingerlike parts of tiny trabecula pass inside the CL.

A dense and large luteal cells are noticed, and a darker thekal cells.

Large luteal cells from granulose contain the secretory granules.

Small luteal cell from theca interna do not contain secretory granules.

Intracellular mechanisms of luteolysis is ischemia (decreased blood flow to CL), and apoptosis.

Macrophages and lymphocytes are present in luteal tissue and increase at the time of luteolysis.

The corpus luteum develops rapidly following ovulation and is also a triangular or pear shaped. It occasionally protrudes as a bottom-like structure 1-2 cm in diameter and 0.5-1 cm in height beyond the ovarian capsule through the ovulation site into the ovulation fossa where it may be palpated around the second day after ovulation. It can not be palpated readily unless the site of the recently ovulated follicle is known, because of the dense tunica albuginea, and the central location of the CL in the mares ovary.

#### Corpus albicans

Cl without the pregnancy regress, becoming over time just a scar-on ovary surface called a corpus albicans, CA.

#### Atretic follicles

The most follicles undergo an involution- involutive or atretic follicles, and can occur at any phase of follicle development.

All the involutive follicles which preserve for a certain time their theca interna are called the cogenic follicles. The theca cells of these follicles as a whole constitute the interstitial gland of overy.

Involution of the corpus luteum, luteolysis, occurs most often in the form of fibrous or fibro-hyalin degen-

eration with cell lysis and marked collagen fibre synthesis, which ends in the formation of a voluminous organelle called-corpus albicans. The process is relatively slow and spread over several weeks.

The vast majority of follicles never develop beyond the primordial stage in the first place. Some of them got as far as the stage of secondary follicle. This one has a remnant of the zona pellucida inside it, but where there once was viable follicular epithelium, scarring has occurred and cells have been removed by necrotization and scavenging.

Also, compared to other mammals, more cystic deviations can be observed in the mare.

Fossa cysts or cysts of germinal epithelium are common and may be palpated in the region of the ovulation fossa in older infertile or non bred mares. These cysts are lined with ciliated columnar epithelium surrounded by dense connective tissue layer.

#### Disscussion

In mammals, ovarian folliculogenesis is a highly selective process during which only a few follicles attain dominant status whereas the majority enters atresia. In each oestrus cycle, the growth and differentiation of dominant follicle(s) involve complex mechanisms, leading to ovulation. These are mainly under the endocrine control of the pituitary gonadotropins follicle stimulating hormnone (FSH) and luteinising hormone (LH), whereas steroids, growth factors and other peptidergig factors are involved as local, paracrine or autocrine modulators of gonadotropin actions. In equine species, little information is available on the composition of follicular fluid and on the physiological modulators of follicular development and maturation. In most domestic mammals, the in vitro maturation rate of oocyte exeeds 90% whereas it remains low in the mare.

In the mare FSH is secreted in a periodic 10 day rhytm of surges, one in late estrus or early diestrus and the other in late diestrus, about 8-12 day of the cycle. Under the stimulus of FSH from the anterior pituitary gland follicles with antrum are stimulated to grow. Those follicles in the first "wave" become atretic about the middle of the estrous cycle because LH is not present to complete their grow, cause ovulation, and the development of the CL (Corpus Luteum). A nonsteroidal protein inhibin and estradiol present in follicular fluid suppress FSH secretion and stimulates LH secretion. Waves of follicular growth and estradiol production occur evry 10 days during the breeding season even though a corpus luteum may be present.

Regresion of the CL around days 14-17 is due to a sharp rise in plasma levels of prostaglandins from the uterus. The luteolysis caused by the uterine production of prostaglandins in the mare is accomplished by transfer of the prostaglandins through the systemic circulation to the ovary rather than the local utero-ovarian pathways described in the cow, sheep and pig.

FSH action early in diestrus may produce a mid – cicle follicle that will sometimes ovulate, but more usually regresses. Around day 13 post-ovulation the endometrium of the uterus secretes PGF2 alfa which causes the destruction ("lycing") of the CL, which will then permit the onset of estrus behaviour. PGF is luteolysin. In mare PGF gets to ovary after going through the general circulation, not in counter current exchange between uterine vein and ovarian artery. Mare ovary is more sensitive to PGF than other species. FSH activity in late diestrus will caused the selection of dominant follicle (or possibly two) which under the influence of increasing estrogen levels early in estrus will develop to reach ovulatory status approximately 21 days after the previous ovulation occurs

It is difficult to compare the mare ovaries. Our experience present that in 10 mares, and 20 investigated ovaries, each of them are different.

Some authors confirm that conclusion, in experiment were examined ovarian mass in tree mares with regular estrous cycle, histological diagnosis of each mass was different (13).

The mares ovary is unique structure which differs from that of other mammals, and the application of three-dimensional internal structure microscopy is convenient for observation of mare ovary (14).

It is typical in the mare that only one follicle is selected from the cohort of follicles, which then continues its growth and becomes dominant. Follicle selection is the mechanism whereby only one of the many available follicles becomes the ovulatory follicle in monovular species and has been a long time mystery in reproductive biology. The largest follicle plays the primary role in further suppressing circulating FSH concentrations to below the requirements of the smaller follicles, which causes their regression.. Results in studies in mares suggested that LH does not influence growth of the dominant follicle until after the beginning of deviation (15).

Some other reports indicate that LH was necessary for continued growth of the largest follicle after deviation, and that the time required for growth of the follicles of the new wave apparently delayed the interval to ovulation after luteolysis (16).

Regressing follicles undergo atresia and in many species apoptosis has been identified as the underlying mechanism in this process. Apoptosis is a form of programmed cell death that is characterized by the activation of endonucleases which leads to fragmentation of DNA. Apoptosis concerning with a cell, and atresia is the term of the complete follicle fate. This indicates that the follicles not destined for ovulation are degenerating as would be expected, that the preovulatory follicles are viable and that the use of apoptosis as an indicator of follicular degeneration in mare is valid (17).

Follicular atresia in the mare appears to be gradual process of which the initiating cause remains unknown. (18).

#### Conclusion

The structure of the ovary of the mare is peculiar and differs from that of other animals in the fact that it does not consist of a cortex (zona parenhimatosa) which contains the vessels and nerves. The internal structure shows a departure from the usual arrangement. The location of cortex and medulla zones is inverted. The follicles and corpora lutea are scattered within the central part of the organ and toward the ovulation fossa. They are enclosed within a dense, richly vascularised connective tissue casing that corresponds to the medulla of the ovaries of other species However, because the ovaries of the mare are conspicuously large, the conventional

histological techniques were unsuitable for the observation of the inside structure of the whole ovary. Concerning the morphology differences in age groups, there is a large variety among them, in general, which make a problem to evaluation. Left and right ovary of young mare (to 2 years old), are similar size and weight, while the left ovary is slightly bigger. Adult (2-8 years), have different ovaries (the left ovary is significantly larger). In old mare, cystic deviations, involution and degeneration is a problem in determination and classification. We could not firmly determine the ovulation frequencies in both ovaries. For that purpose, a further serial investigation have to be done.

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# SEZONALNOST, FOLIKULOGENEZA I LUTEOGENEZA U JAJNICIMA KOBILE

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Kratak sadržaj. Godišnji ciklus parenja konja je u značajnoj zavisnosti od fotoperiodičnih promena. Ovakvi podsticaji iz okoline bivaju prevedeni u endokrine signale u habenulo- pinealnoj žlezdi. Kod kobile, kratko trajanje dnevne svetlosti je povezano sa opadanjem lučenja gonadotropina što dovodi do posledičnog opadanja aktivnosti jajnika. Jajnik kobile je jedinstvene strukture i razlikuje se od jajnika ostalih sisara. Jajnici su sečeni u oblasti fose ovulationis, i potom analizirani u sezoni parenja kod kobila (10), tokom estrusnog ciklusa (mart-juli). Tkivni isečci su

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fiksirani u Bujen fiksativima, a zatim bojeni Hematoksilin-eozinom. Posmatrani su odnosi i relacije rasporeda kore, srži i fose ovulationes. Ovulatorna fosa je lokalizovana u centru jajnika i okružena gustim ovarijalnim korteksom. Srž je razmeštena u uskoj zoni na periferiji. Područje kore koja okružuje fosu ispunjeno je folikulima u razvoju. Posmatrani su folikuli različitih veličina i utvrđivani su odnosi ovocita i okolnih ćelija. Unutrašnja šupljina oslobođenog folikula brzo se ispunjava krvlju obrazujući hemoragično telo od koga će se formirati lutealno tkivo. Kobila ima najveće žuto telo u poređenju sa drugim životinjama. Ono je kruškoliko- trouglastog oblika, veličine oko 0,5-1 cm, i obavijeno gustom tunikom albugineom, smešteno u unutrašnjosti fose.

Mehanizmi regulacije sezonalnosti su pod snažnim uticajem i povezanosti između hipotalamo- pituitarno- gonadalne sprege i mi smo razmatrali rezultate imajući u vidu početak ciklusa reproduktivnih aktivnosti u toku ranog proleća.

Ključne reči: sezonalnost, ovarium, kobila, reprodukcija, folikulogeneza, luteogeneza