Reproductive Anatomy and Physiology of the Mare

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Regardless of how involved you are in horse breeding — whether you own one beloved mare and wish to raise its foal, or manage a large-scale breeding farm and supervise the breeding of hundreds of mares each year - a working knowledge of the mare's reproductive anatomy and physiology is essential. This knowledge provides the fundamental basis on which all other principles of horse breeding rest.

FEMALE REPRODUCTIVE ANATOMY

The mare's reproductive tract lies in a roughly horizontal position within the abdominal and pelvic cavities. It includes the vulva, vagina, cervix, uterus, oviducts and ovaries. Each portion of the tract plays an essential role in reproduction. Changes in the anatomy or interruption in the function of any section can contribute to reproductive problems (Figure 1).

VULVA

The vulva is the exterior opening to the reproductive canal. It consists of the labia, clitoris and the vestibule. The construction of this region is important because it serves to protect the mare from the entrance of air and other contaminants into the vaginal vault.

The labia are the lips of the vulva, which meet in a 5- to 6-inch vertical slit located below the anus. Their vertical positioning, plus labial muscle tone, helps to keep the lips tightly closed, sealing the vestibule from the external environment. In normally conformed mares, approximately 80 percent of the opening in the vulva lies below the pelvic floor. The projection of the pelvis' ischium bone denotes the pelvic floor and can be felt upon insertion of a finger into the vulva. If the pelvic floor is positioned low relative to the labia, the anus tends to retract forward (anterior) and the upper part of the vulva becomes horizontal, especially with increased age. The platform formed by the perineum (the skin between the anus and the vulva) and the upper part of the vulva collects feces and creates a conformation which encourages breaching of the labial seal. When this occurs, air and debris can be sucked into the internal reproductive tract. This condition is known as pneumovagina, or wind-sucking. The pelvic conformation predisposing a mare to this defect may be inherited and, therefore, cannot be altered. However, the vulva can be artificially sealed by suturing the labia together, a procedure which is known as an episoplasty (Caslick operation).

The clitoris is a small knob-shaped structure located inside the labia and on the floor of the vulva. It can be plainly seen during estrus when the mare exhibits eversion of the vulva (winking), and following urination.

The vestibule is the internal portion of the vulva and extends about 4 inches into the interior. It is separated from the vagina by a fold of tissue which includes the hymen. This fold is located just forward of the urethral opening. The hymen is often intact in maiden mares, and may be so thick that it must be ruptured surgically prior to first mating to avoid physical and psychological trauma to the mare. Glands within the vestibule secrete mucus which lubricates and protects the vulva and vagina.

VAGINA

The vagina consists of a 6 to 8-inch long muscular, mucus membrane-lined tube which communicates the vestibule of the vulva to the cervix. The vaginal tissues must be extremely elastic and distensible to accommodate the penis in breeding and the foal during birth.

CERVIX

Basically a highly distensible muscle, the cervix acts as a physical barrier between the vagina and the uterus. The cervix is approximately 4 inches long and appears as a circle of folded tissue at the anterior surface of the vaginal vault. Its shape and characteristics change significantly in response to the body's hormonal environment. In response

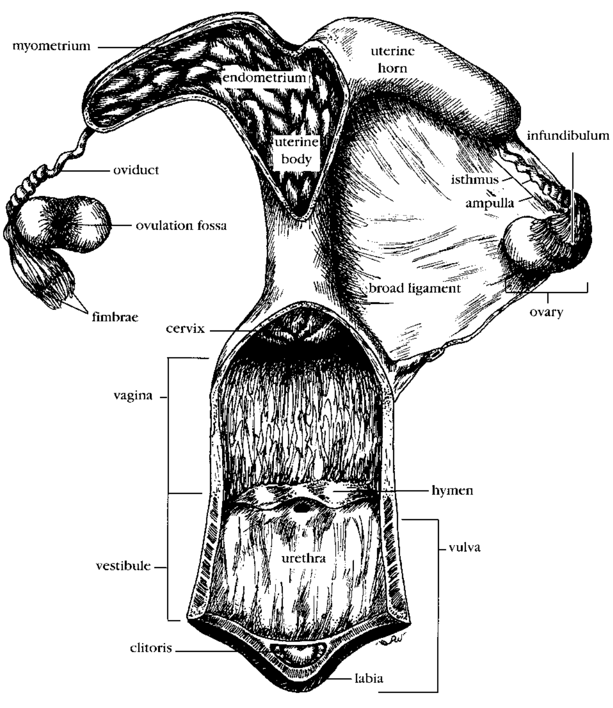


Figure 1: Reproductive tract of the mare

to increased estrogen produced during estrus, the cervix appears pink due to increased vascularity. During this period, it produces abundant thin, watery mucus and is so relaxed that it is often found lying limply on the vaginal floor. This flaccid cervical tone facilitates passage of semen or breeding instruments directly into the uterus. During live cover the diestrous period and pregnancy, it appears blanched, produces a thick, sticky mucus, is tightly closed and held in the center of the vaginal wall. The physical barrier produced by a healthy cervix provides a major line of defense against uterine contamination and infection. Consequently, damage to this structure can result in significant problems in maintaining fertility (Figure 2).

Figure 2: Changes in the equine cervix during the estrous cycle. The equine cervix as seen through a vaginal speculum during diestrus (left) and estrus (right). Under the influence of progesterone during diestrus, the cervix is tightly closed and surrounded by firm, well-defined folds. During the estrogen-dominated period of estrus, the cervix is swollen, with relaxed folds which hang down over the open orifice.

UTERUS

This is a multi-layered, hollow, Y-shaped organ. The base of the Y is called the uterine body, while the two branches are called the horns. The uterus is suspended within the body cavity by two tough, sheet-like structures called the broad ligaments. Sagging of these ligaments with age, parity or trauma can cause a downward tilting of the uterus. This conformation can predispose the mare to the backwash of urine (urine pooling) into the reproductive tract and its accumulation at the cervix. Urine pooling can cause uterine infection and poor fertility.

The uterus is composed of three distinct layers. The outermost, serous layer is continuous with the broad ligaments. The middle layer consists of two sheets of muscular tissue, one oriented longitudinally and one circularly. This is called the myometrium and is responsible for the powerful contractions which expel the foal at birth. The endometrium is the innermost layer. It is a complex mucosal membrane containing a rich blood supply and many glands.

The character of the uterus is profoundly influenced by the hormones acting upon it. During estrus, estrogen causes a swelling and increased folding in the endometrium. This increased water retention can be felt or seen during a transrectal pelvic exam performed either by manual palpation or by ultrasonography. Progesterone secreted during diestrus encourages glandular development and secretion in the endometrium. It also encourages greater muscular tone within the myometrium. This tone is apparent upon pelvic examination, and is particularly pronounced during early pregnancy.

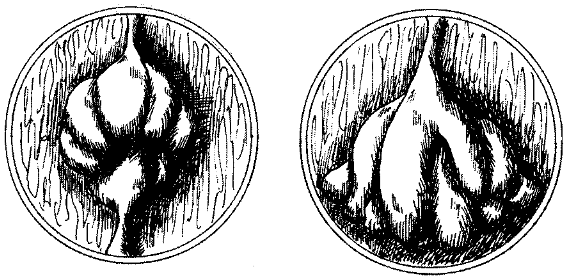
The ultimate function of the uterus is to protect, nourish and provide an environment conducive to the development of the embryo and fetus, and to expel the fetus during birth. Maintaining healthy tissues within the endometrium is crucial for optimal fertility. In fact, endometritis (uterine infection) is a major cause of infertility in mares.

OVIDUCTS

Also known as Fallopian tubes, the oviducts are tiny, highly coiled tubes. Each connects the tip of a uterine horn with an ovary. The ovarian end of the oviduct is called the infundibulum. It is enlarged and shaped like a catcher's mitt with finger-like projections from its end called fimbriae. This design serves to cradle or envelope the portion of the ovary from which the ovum (egg) will emerge, so that it can be captured and transported down the oviduct to the uterus. Fertilization of the ovum occurs in the oviduct, in the area below the infundibulum known as the ampulla. The final portion of the oviduct, where it narrows to join the uterus is called the isthmus. The oviducts are heavily lined with hairlike projections called cilia, which beat rhythmically. The cilia, as well as the muscular layers lining the oviducts, are responsible for transporting the ovum down the oviduct and for moving sperm in the opposite direction.

OVARY

The ovaries of the mare are unique both in shape and make-up. They are kidney bean-shaped, and vary in size and texture between the breeding and non-breeding seasons. During the summer, they are active and about the size of a tennis ball. The convex side of the ovary is called the hilus. It is the area of attachment to the abdominal



cavity. The blood vessels and nerves which serve the entire ovary pass through this region. The concave side of the ovary contains an area unique to the mare, the ovulation fossa. This wedge-shaped area is the only portion of the ovary from which ova may be shed (ovulated). The inner structure of the ovary consists of two layers. These are arranged "inside out" from that found in other farm species. The outermost area of the equine ovary is called the medulla. The nerves and blood supply to the ovary issue from here, but there are no ova. The cortex makes up the inside of the ovary. This is the area which contains the ova (eggs). When a filly is born, the ovarian cortex already contains a full complement of oocytes (egg cells). No new ova will be produced after this time. The cortex supports the growth and development of the structures on the ovary which help the eggs mature and which secrete hormones that help to control the reproductive process.

One of these cortical structures is called the follicle. Each ovum is encased by a single layer of follicular epithelial cells. This structure is called a primordial follicle. Of the hundreds of thousands of primordial follicles present in the ovary at birth, only a small fraction will ever reach maturity and liberate their ova (ovulate). Most follicles degenerate and undergo partial development and then disappear. Upon appropriate stimulation, a primordial follicle will begin to grow and mature in preparation for ovulation. This follicular growth process involves enlargement, development of cellular layers (granulosa, theca interna and theca externa) around the follicular wall and accumulation of fluid within the central follicular cavity. Among other functions, the cellular layer produces the hormone estrogen. As the enlarged preovulatory or Graafian follicle nears maturity, it bulges from the ovary's surface. This bulge can be felt through the rectal wall when the mare's ovaries are manually palpated. Ultrasonic images of the preovulatory follicle appear as a black area within the grayish tones of surrounding ovarian tissues. The follicle's diameter indicates its maturity. Those 35 millimeters or greater are considered capable of ovulating. Another cortical structure, the corpus luteum, forms from the tissues remaining after a follicle ruptures at ovulation. Unlike the follicle, the corpus luteum is solid-cored and secretes the hormone progesterone. This difference in construction can be recognized as a change in texture by an experienced practitioner during rectal palpation, and by its ultrasonic image which is ectogenic (gray).

PHYSIOLOGY OF REPRODUCTION

The reproductive efficiency of the horse is the lowest of all of our domestic animals. The national average for live foals versus bred mares in human-controlled horse breeding is around 50 percent. To be sure, the mare is perplexingly unique in many of her approaches to reproduction, both behaviorally and physiologically. Perhaps this can account for some of her notorious inefficiency. However, human intervention in the breeding process has certainly played a substantial role in attaining this dismal state of affairs. The consensus among equine reproduction researchers and professionals is that the leading cause of infertility in mares is human management. It is interesting to note that horses can reproduce quite well when left to their own devices. Live foal rates in wild (feral) horse populations often reach 80 to 90 percent efficiency.

One reason for poor reproductive performance is the fact that few horse breeders select their breeding stock for reproductive efficiency. Stallions and broodmares are selected for what they have accomplished athletically, for their pedigree, or for their beauty. A mare who is valuable by these standards, but who is not an efficient producer, will often be kept, coddled and coaxed into conceiving, often at great expense, rather than culled. Another negative aspect of human management is that we frequently attempt to breed mares outside of their natural reproductive season. Left to their own devices, mares normally mate during the longer, warmer days of spring and summer. Combined with their unusually long 11-month gestation period, Mother Nature has provided them with conditions in which foals will be born when their chance of survival is maximized. Unfortunately, many horse breed registries have decided that the universal birthdate for horses should be January 1 of each year. Therefore, in order to gain a developmental advantage for their product, which may be expected to compete with others at an early age, many breeders try to have their broodmares foal as close to January 1 as possible. This requires getting mares in foal in February when most are not physicologically capable of reproducing under natural conditions.

SEASONAL POLYESTRUS

During the nonreproductive (winter) season, most mares are in a state of reproductive quiescence (or hibernation) called anestrus. During this time, they will not respond to the stallion's attention, their ovaries do not develop any structures, and there is minimal ovarian hormone secretion. The situation is very different during the spring and summer. During this season of reproductive activity, the mare will experience a series of estrous cycles. These cycles will repeat themselves at 21 to 23-day intervals until pregnancy occurs or until she reverts back into anestrus with the advent of winter. Because she undergoes estrous cycles only during a circumscribed portion of the year, the mare's reproductive habits are termed seasonally polyestrus.

REPRODUCTIVE BEHAVIOR

There are two different stages to the estrous cycle. These are generally distinguished by the mare's behavioral responses to the stallion. Estrus (heat) lasts an average of 5 to 7 days. Interestingly, the mare has the longest heat period of any domestic animal. Estrus is characterized by receptivity to the stallion. A mare showing classical estrous behavior will adopt a urination stance - squatting with legs spread and tail raised. She will lean into the stallion, urinate small volumes frequently, and expose her clitoris by everting her vulva (winking). Most mares cease estrous behavior within 24 to 48 hours following ovulation. This marks the beginning of the other stage of the cycle, know as diestrus, which lasts an average of 14-16 days. During diestrus, the mare rejects the stallion with behavior typically seen in the form of tail switching, squealing, striking, biting and/or kicking.

These behaviorally defined divisions in the estrous cycle roughly parallel the events which are occurring in the ovary during what is termed the follicular phase and the luteal phase. However, these latter two phases are defined by the endocrine (hormonal) events punctuating the estrous cycle.

ENDOCRINOLOGY OF REPRODUCTION

The processes involved with reproduction in the mare are driven by the action of substances known as hormones. Hormones are chemicals which are produced by various tissues in the body and which travel through the circulatory system to produce an effect on one or several target organs. The study of hormones and their effects is called Endocrinology.

The control of reproduction is precise, richly complex and elegant, like a fine symphony. The pelvic reproductive organs (ovaries, oviducts and uterus), are only players in this orchestration of interactive events. The conductor is the hypothalamus. It is located far from the abdominal cavity, deep within the tissues of the mid-brain. The hypothalamus is responsible for receiving and interpreting messages from many sources, both intrinsic and extrinsic, and coordinating their signals to produce the desired effects. The hypothalamus is capable of exerting moment-to-moment control over the events occurring during each estrous cycle, as well as long-term control over seasonal reproduction.

The hypothalamus interprets environmental cues, such as day length, temperature and other factors, through input from other brain centers. At the appropriate time, it signals the start of the reproductive season by producing a chemical signal in the form of gonadotropic releasing hormone (GnRH).

When secreted at particular concentrations and frequencies, GnRH stimulates another portion of the brain called the pituitary (hypophysis). The pituitary is a small gland located at the base of the brain. It is attached to the hypothalamus by a stalk containing both blood vessels and nerves which serve as its pathway for communication with the hypothalamus. In response to the stimulus from GnRH, the anterior portion of the pituitary (adenohypophysis) releases two gonadotropic hormones, Follicle Stimulating Hormone (FSH) and Luteinizing Hormone (LH). These two hormones are responsible for stimulating the gonads (ovaries in the mare, testes in the stallion) in several ways. The posterior pituitary (neurohypophysis) has also been implicated in the control of seasonal reproduction through its production of the hormone prolactin. However, little is yet known about the precise control or actions of this hormone.

FSH stimulates the growth of follicles. An increase in circulating levels of FSH has been noted during mid-to-late diestrus. This corresponds to the time of initial follicular development prior to the next estrous period. A group of small to medium-sized follicles begin to grow as diestrus progresses, but eventually only one (or two) dominant follicle(s) is selected to continue its development to ovulation. When follicles reach a certain stage of development (approximately 20 to 25mm in diameter), they begin to secrete the steroid hormone Estradiol-17B, which is a specific form of estrogen. Estrogens cause the familiar receptive behavior patterns observed in mares during heat and act to prepare the uterus for receiving the conceptus (embryo) if fertilization occurs. Estradiol concentrations continue to rise throughout estrus, peaking immediately prior to ovulation. It is this high concentration of estradiol circulating throughout the body which reaches the brain and stimulates the release of LH.

Luteinizing Hormone is responsible for stimulating ovulation and supporting the initial stages of corpus luteum development. The pattern of LH secretion in the mare differs from that of other domestic animals. LH is secreted for a prolonged period of time in the mare, beginning shortly before or at the initiation of behavioral estrus, reaches peak concentrations two days following ovulation, and declines back to baseline during the early portion of the luteal phase.

Ovulation generally occurs toward the end of estrus. Therefore, elongation of the estrous period, which is encountered most often during the seasonal transition, occurs prior to the time of ovulation. It is important to realize that estrus is a behavioral event while ovulation is a physical event. Although estrus and ovulation normally occur together, ovulation is not dependent upon estrus, nor does estrus ensure ovulation.

The completion of ovulation ushers in the luteal phase of the estrous cycle. After ovulation, the remaining tissues of the ruptured follicle undergo a rapid conversion into a corpus luteum (CL). This conversion begins immediately following ovulation with the empty follicular cavity accumulating coagulated blood and forming the precursor to the CL known as the corpus hemorrhagicum. Luteal cells begin to proliferate around the walls of the corpus hemorrhagicum and grow toward the interior, eventually replacing the clotted blood with a solid core of luteal cells. When this is achieved, the structure is called a corpus luteum.

The luteal cells within the corpus hemorrhagicum and CL secrete another steroid hormone called progesterone. In the uterine endometrium progesterone stimulates the development of the glands and tissues required for maintaining the pregnancy. Circulating progesterone reaching the brain acts to inhibit the release of LH from the pituitary. Progesterone changes the mare's behavioral pattern into that typical of diestrus. The mare is unusual in that she will not show signs of estrus as long as progesterone is circulating in her system, regardless of the amount of estrogen which is present. Therefore, if the mare does not conceive during the present estrous cycle, progesterone production must be halted in order for the estrous cycle to repeat.

This is accomplished through the action of still another hormone called prostaglandin F 2a (PGF 2a). If the mare is not pregnant, PGF 2a is released from the uterus 14 to 16 days following ovulation. It travels to the ovary where it causes destruction of the CL by a process known as luteolysis. Luteolysis marks the end of the luteal phase and the beginning of the follicular phase of the cycle. After the CL is lysed and progesterone declines, the mare is free to return to heat, as the cycle begins again (Figure 3).

SEASONALITY

The primary environmental cue used in regulating seasonal reproductive activity is the length of daylight. The length of the photoperiod is interpreted by the system through neural signals to specific portions of the brain and then given endocrine expression through production of a hormonal message. Part of this message is carried in the form of melatonin. Melatonin is produced by the brain's pineal gland in response to the absence of light. Therefore, during the short days (and long nights) of winter, more melatonin is produced than during the summer. Melatonin has a suppressive effect upon GnRH.

During anestrus, when melatonin levels are high, the GnRH secretion pattern is not stimulatory to the pituitary. LH concentrations, therefore, are minimal. Surprisingly, levels of follicle stimulating hormone (FSH) do not appear to change with the seasons. The mechanism controlling seasonal FSH secretion is not yet understood. The ovaries are small and hard in anestrus, with no significant follicular activity or hormone production.

The process by which the complex interplay of cyclic events is initiated in the spring and is continued in the fall is still the subject of much investigation. Of the two transitional periods, the spring has received the most scientific attention, reflecting the breeding industry's desire to produce early-season foals.

As the days grow longer in the spring, the mare's reproductive organs begin to activate. This is a long process which involves several weeks of erratic and unpredictable reproductive activity. The first measurable changes noted during early spring transition are a decrease in melatonin production and increases in the secretion of GnRH and prolactin. This is followed by ovarian recrudescence which takes the form of repeated waves of follicular growth, without ovulation, followed by atresia. Rises in estradiol concentrations accompany the follicular growth waves later in the transition. LH concentrations do not rid until immediately before the first ovulation of the season. The first ovulation of the spring ushers in the season of stable estrous cycles. Reproduction again begins to become erratic as the days grow shorter in the autumn, as mares begin the transition into anestrus.

Thanks to the efforts of many fine researchers, much has been learned about the mare's reproductive controls. But, in a field of study in which chemical changes of a few billionths of a gram are capable of provoking radical physical and physiological shifts, much still remains a mystery.

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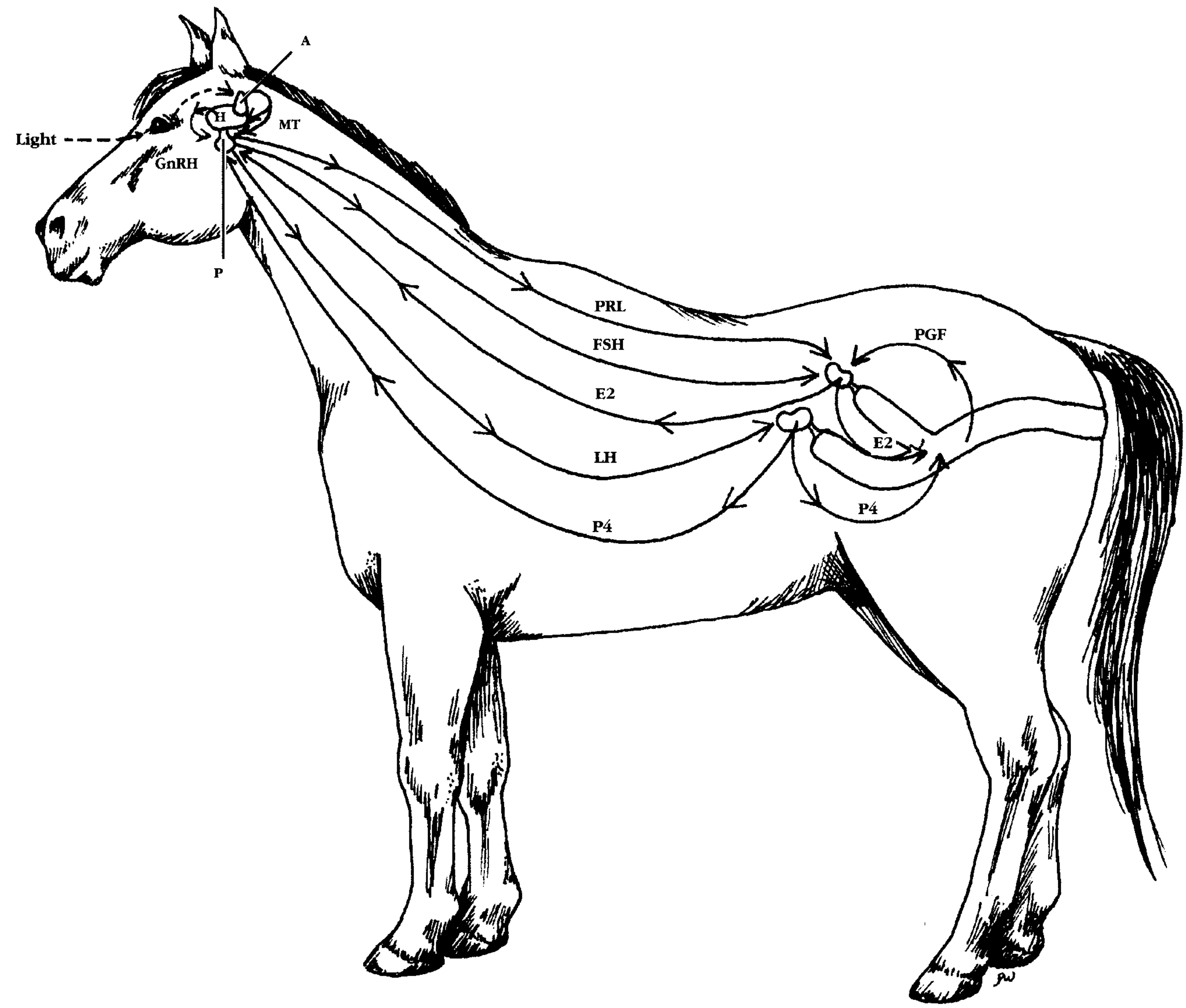

Figure 3: Endocrine events controlling reproduction in the mare. Photoperiod is interpreted through the **pineal gland** (A). **Melatonin** (MT) is released during dark phases. Decreased melatonin during the longer days (shorter nights) of spring is interpreted as a positive stimulus by the **hypothalamus** (H). **Gonadotropic Releasing Hormone** (GnRH) is released in stimulatory quantities/patterns. The **pituitary** (P) releases prolactin (PRL) in response to unknown stimuli in the early transition. Prolactin is associated with early follicular growth. Later in the transition, GnRH stimulates the pituitary to release the gonadotropins, **luteinizing hormone** (LH) and **follicle stimulating hormone** (FSH). FSH encourages follicle growth. Large follicles secrete **estradiol** (E2), which stimulates endometrial growth and pituitary release of LH. Ovulation followed by corpus luteum production is regulated though LH. The corpus luteum produces **progesterone** (P4) which stimulates the endometrium and inhibits further gonadotropin release from the pituitary. If pregnancy is not achieved, **prostaglandin** $\mathbf{F_{2\,a}}$ (PGF) is released from the uterus and causes luteolysis. The cycle begins again.

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