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CLINICAL REVIEW

NORMAL FELINE REPRODUCTION
The queen

Aime K Johnson

Practical relevance: Cats are seasonally polyestrous, meaning they exhibit multiple estrous cycles within a season, followed by a period of non-cyclicity. Cats cycle when the day length is long but can be induced to cycle year-round with 14 h of continuous artificial lighting. The feline estrous cycle includes the following stages: proestrus, estrus, interestrus and, if ovulation occurs, diestrus. Cats are induced ovulators and ovulate in response to multiple natural matings. Successful breeding in a cattery requires knowledge of the female's reproductive cycle, behavior and management, and often improper management can be the sole cause of infertility.

Aim: The aim of this review is to provide readers with an overview of normal anatomy, cyclicity, management and behavior of the queen. It includes a series of questions veterinarians can ask to obtain a baseline knowledge of the management of the specific breeding set-up.

Evidence base: The information in this article is based on the author's experience, as well as drawing on historical and current literature, and provides the most up-to-date review as possible.

Keywords: Female anatomy; puberty; estrous cycle; cattery management; breeding management

SERIES OUTLINE

This article forms part of a series of evidence-based reviews on feline reproduction and reproductive problems, written by key opinion leaders. An outline of the series is included at: bit.ly/JFMSreproduction

Anatomy

For a diagram of the reproductive anatomy of the queen, see Figure 1.

Ovaries

The queen has two ovaries, which typically measure around 1 cm x 0.5 cm. They can be visualized by ultrasound just caudal to the caudal pole of each kidney. The ovaries are suspended in the abdomen by a portion of the broad ligament called the suspensory ligament of the ovary. The ovaries are only partially covered by a thin ovarian bursa originating from the mesosalpinx, the portion of the broad ligament that suspends the oviducts. The ovaries are connected to the uterine horn by the proper ligament of the ovary. The ovarian artery supplies blood to the ovaries and originates from the aorta. The ovarian vein takes blood back to the caudal vena cava from the ovary, oviducts and cranial uterus.

Puberty

Puberty in the queen occurs between 6 and 12 months of age and at a weight greater than 2–3 kg (or approximately 80% of adult weight). Age at puberty will depend on the time of the year the kitten was born, as well as specific breed variations. Longhair cats tend to reach puberty at a later age than shorthair cats.[1] Smaller breeds tend to reach an earlier puberty than larger breeds. A kitten that is born in the spring and reaches 6–8 months during the short days of the year may not enter puberty until the following breeding season when the day length increases.

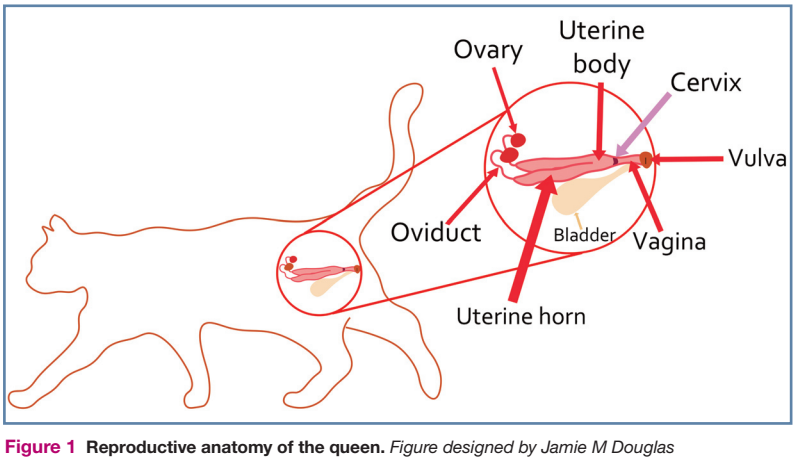

Figure 1 **Reproductive anatomy of the queen.** *Figure designed by Jamie M Douglas*

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Oviducts

The oviducts are long and tortuous, measuring 5–9 cm in length. They are comprised of the fimbria, infundibulum, ampulla and isthmus, and are suspended by the mesosalpinx portion of the broad ligament.[2] Fertilization occurs at the ampullary–isthmus junction, where the sperm travelling through the isthmus meet the oocytes at the edge of the ampulla. The oviduct enters the uterus and terminates in a small mound (or papilla) of smooth muscle.[3]

Uterus and cervix

The uterus of the queen is bicornuate, comprising a short (2 cm) body and two long horns (7–10 cm, depending on the maturity of the queen, previous litters and stage of the cycle). Its blood supply is from the uterine artery, which branches off the vaginal artery. Blood leaves the uterus via the uterine vein, which leads to the internal iliac vein.[4]

On ultrasound examination, the uterine body can be visualized dorsal and slightly caudal to the bladder and the horns can be followed on each side of the bladder cranially. The uterine horns in a postpubertal queen measure 1 cm or less in diameter (Figure 2) and should be free of fluid. On ultrasonography, when in cross section, the serosal surface of the uterus appears as a hyperechoic ring surrounding a less hyperechoic but homogeneous uterine endometrium.

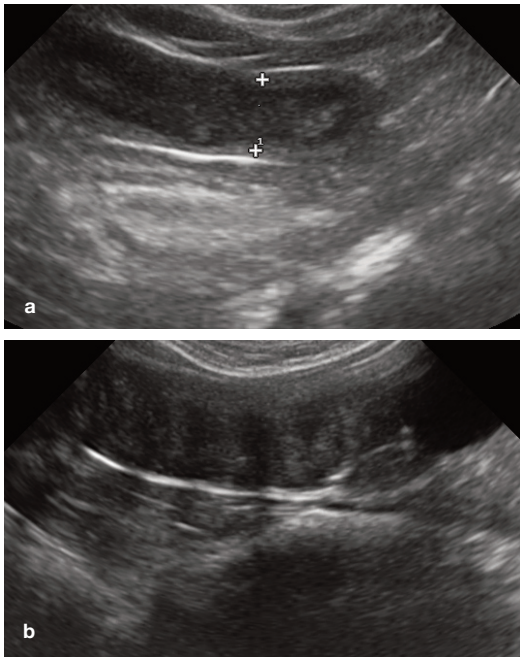

Figure 2 (a) Ultrasound image of a normal postpubertal queen. The uterus (between the measuring calipers) is imaged longitudinally and measures 0.78 cm in diameter and is of normal echotexture. (b) Ultrasound image of a postpubertal aged queen with cystic endometrial hyperplasia. The uterus is imaged longitudinally. The uterine folds are prominent and can be observed as light and dark striping within the uterus. Although not shown, the uterus measured 1.4 cm in diameter in this queen, which had presented for subfertility

Transcervical insemination of the queen can be difficult as the vaginal diameter may be as thin as 1 mm.

The myometrium, located between the serosal surface and the endometrium, cannot be easily differentiated from the endometrium by ultrasound unless pathology is present. The lumen of the uterus appears as a thin hyperechoic line.[5] The uterine body leads caudally to the cervix. The cervix is difficult to visualize via ultrasound since it is so far caudal but consists of a thickened muscular area. The external os of the cervix extends into the cranial vagina and points in a ventrocaudal direction.

Vagina and vestibule

A vaginal fornix is located in the vagina cranial to the cervical opening. Just caudal to the cervix, and located on the dorsal portion of the vagina, is the dorsal median fold. The prominence of this fold changes during the phases of the estrous cycle and is greatest during estrus. Partly due to the prominence of the fold, the vaginal diameter decreases and the length of the fornix increases during estrus.[6] Based on this, transcervical insemination of the queen has been difficult to master as the vaginal diameter may be as thin as 1 mm.

The vestibule connects with the vaginal vault with no distinct hymen. The diameter of the vestibule is much greater than the vagina (about 4 mm) and this structure is approximately 2 cm in length.[6] The vestibule ends caudally with the vulva, which consists of two dorsal labia. When in estrus, the vulva becomes slightly edematous, but it is not as prominent as in the dog. The clitoris is located just inside the vulvar labia in the clitoral fossa and on the ventral aspect of the caudal vestibule. The clitoris is analogous to the penile tissue in the male and may be enlarged in cases of chronic irritation or certain disorders of sexual development (intersex conditions). Figure 3 shows the complete uterine tract of a queen in diestrus, as determined by the corpora lutea on the ovaries and the tortuous uterine horns.

When in estrus, the vulva becomes slightly edematous, but it is not as prominent as in the dog.

Cyclicity

The queen is seasonally polyestrous, meaning there will be multiple cycles within a season followed by a period of non-cyclicity (anestrus). The queen cycles during the longer day lengths and cyclicity will cease when the day length is short. In the USA, queens cycle during the spring and summer (about March to September) and cyclicity stops as the days shorten in the late fall and winter (October to February). Cyclicity may vary in different parts of the world depending on latitude and photoperiod, with queens sometimes exhibiting resumption of heat cycles as early as January. Some queens may exhibit year-round cyclicity under natural lighting and do not display a seasonal anestrus, but it

Figure 3 Complete reproductive tract of a normal queen in diestrus, with the caudal tract opened to show the luminal anatomy. The red arrow indicates the urethral opening and the urinary bladder can be visualized just above the arrow. The vestibule has a larger diameter caudal to the urethral opening and the vagina narrows as it approaches the cervix (green arrow). The uterus is partially opened through the body and base of each horn to show the normal endometrium. The remainder of the uterine horn is toned and tortuous, indicating diestrus and the influence of progesterone. Several corpora lutea can be seen on the ovary on the right (white arrows)

is difficult to predict which cats will continue to cycle. Exposure to 14 h of artificial lighting for at least 2 months will induce and maintain cyclicity. If the lighting duration is reduced to 8 h, cyclicity will stop and the queen will enter an anestrus period. Exposure to 24 h of light will maintain cyclicity but the number of heat cycles has been shown to decrease from two per month (with 14 h of light) to one per month.[7] Exposure to a 14:10 light:dark schedule will provide year-round cyclicity; but, in this author's experience, overall pregnancy rates may still decrease slightly during the winter months despite supplemental lighting. Queens housed in a home setting are typically exposed to a combination of artificial and natural lighting, but the lighting is often not consistent enough to maintain cyclicity year-round.

The queen is an induced ovulator and ovulates following coitus (see box on page 208). Spontaneous ovulation (ovulation without coitus) may occur in approximately one-third of cats.[8] Incidence of spontaneous ovulation increases as body weight increases.[8] Although factors affecting spontaneous ovulation are not clearly known, this author sees it more commonly in cats housed within the visual, olfactory and auditory presence of an intact male. This has also been observed in other group-housed queens; in one study, the incidence of spontaneous ovulation prior to the addition of a male was 0–22%, compared with 33–57% after a male was housed in a separate cage within the room.[9]

Stages of the feline estrous cycle

The stages of the feline estrous cycle are proestrus, estrus, interestrus, diestrus and anestrus (Table 1 and Figure 4).

Proestrus

Proestrus is often not observed in cats due to the short duration (typically less than 24 h) and vague behavioral signs. Proestrus is associated with preparation for estrus where follicle size is increasing, estrogen concentrations are rising and the vaginal epithelium is thickening. On vaginal cytology (see 'Obtaining a vaginal swab' description on page 210), proestrus is identified by <50% cornified cells and mainly small to large and intermediate cells.

Table 1 Phases of the estrous cycle in the queen, with discriminating features

Stage of cycle	Length (days)	Clinical and behavior changes	Cytology	Other features
Proestrus	<1	Vulvar swelling, rubbing, vocalization. Does not accept male	<50% cornified cells; mainly small to large and intermediate cells	–
Estrus (follicular phase)	5–7 days	Vocalization, rubbing on objects, elevating hindquarters. Accepts male	>75% cornified cells (often with nucleus); large intermediate cells	Phase shortened by mating; longer if no ovulation occurs
Interestrus	8–9 days	No hormonal activity; therefore, no estrous behavior, no vocalization and vulva normal	<50% cornified cells; large intermediate and parabasal cells	Previous follicles regress; new follicular wave begins, starting proestrus and estrus again
Diestrus – pseudopregnancy (shortened luteal phase)	40–45	No estrous behavior for the entire period	Small intermediate and parabasal cells	Corpora lutea regress at around 40 days, allowing cyclicity to resume
Diestrus – pregnancy (luteal phase)	63–65	No estrous behavior for the entire period	Small intermediate and parabasal cells	Corpora lutea remain until parturition. Phase ends when kittens are delivered
Anestrus	Several months	No hormonal influence, no estrous behavior	Scattered small intermediate and parabasal cells	Short days, no ovarian activity

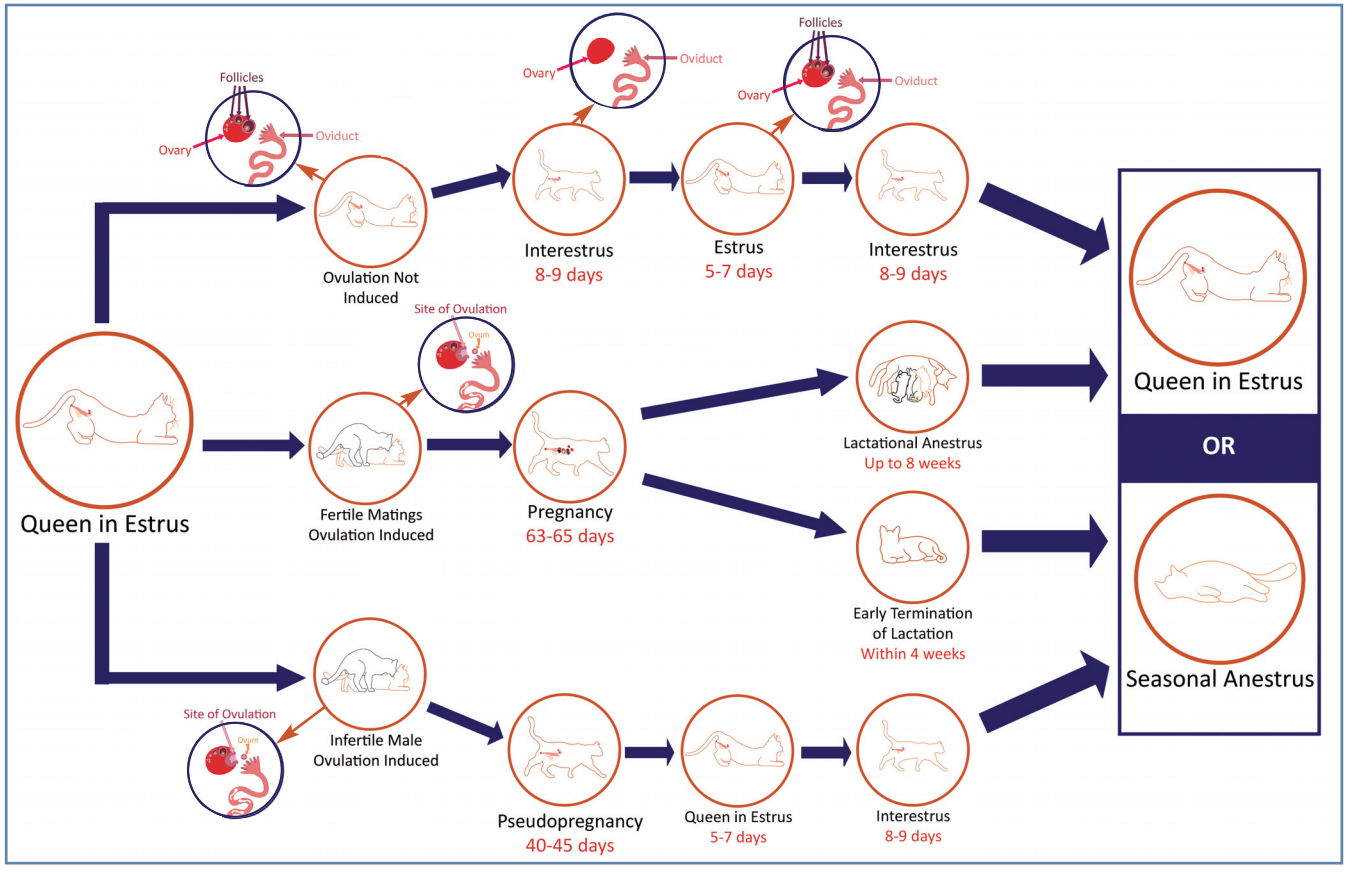

Figure 4 **Diagram showing the progression through the feline estrous cycle.** *Figure designed by Jamie M Douglas*

Estrus (follicular phase)

The estrus phase (heat) is characterized by increasing estradiol (>20 pg/ml) from the growing follicles, receptivity to the male and acceptance of coitus. This phase, also referred to as the follicular phase, averages 5–7 days (range 2–19 days).[10] During estrus, the vaginal cytology will increase to >75% cornified epithelium, but intermediate cells may remain visible, and cornification may not reach 100%, as it does in the dog (Figure 5). The nucleus of the cells becomes pyknotic, but typically will not disappear completely. Red blood cells are rarely observed in the vaginal cytology unless caused by mucosal irritation when obtaining the swab. Neutrophils are rare but may appear for a short time as the queen enters interestrus.

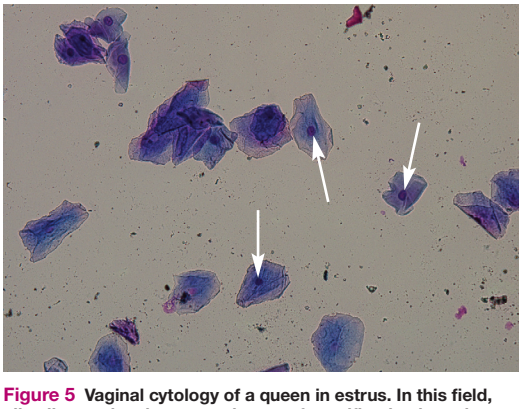

Figure 5 **Vaginal cytology of a queen in estrus. In this field, all cells are showing some degree of cornification based on the rough, irregular cell border and flattened appearance. Approximately half of the cells have retained nuclei (arrows), but these are small and dark, indicating pyknosis**

Figure 6 **Gross specimen from a queen in estrus at the time of ovariohysterectomy. Three follicles can be seen on the surface of the ovary (arrows) and measure 2–3 mm each**

During estrus, the growing follicles reach maturity and measure 2–3 mm in diameter (Figure 6). Each ovary will generally contain between three and six mature follicles during each follicular wave. Estrus behavior typically involves rubbing of the neck and face on walls and furniture, rolling on the back, vocalization, lordosis position and treading with the hind feet with the rear quarters elevated. Behavioral signs of estrus often lag behind the actual onset of the estrus phase. In an early study, only 8% of queens showed behavioral signs on day 1 of estrus, but this percentage gradually increased, with 80% of queens showing estrus behavior by day 4 and 100% by day 6.[10] If mating occurs prior to the maturation of the follicles, ovulation is not likely to occur.

During estrus, cornification on vaginal cytology may not reach 100%, as it does in the dog.

Estrus after pregnancy and lactation
A fertile estrus will occur approximately 10 days after weaning. Nursing kittens cause a negative feedback on cyclicity and queens will experience a lactational anestrus. Queens with smaller litters (and less nursing stimulation) or queens that have lost their litter will show their first estrus 10 days after parturition.[1]

Interestrus

If ovulation does not occur, the interestrus phase follows estrus. The length of interestrus varies with individual cats, but averages 8–9 days.[10] During interestrus, the dominant follicles undergo atresia and estradiol decreases. The vaginal cytology will decrease to <50% cornified epithelial cells and will contain mainly parabasal and intermediate cells (Figure 7). It is important to note that cornified epithelial cells are often still observed throughout the interestrus phase but will remain fewer than half of all cells present. As one set of follicles is reducing, the next wave of follicular development is already well under way. Interestrus then transitions back into estrus.

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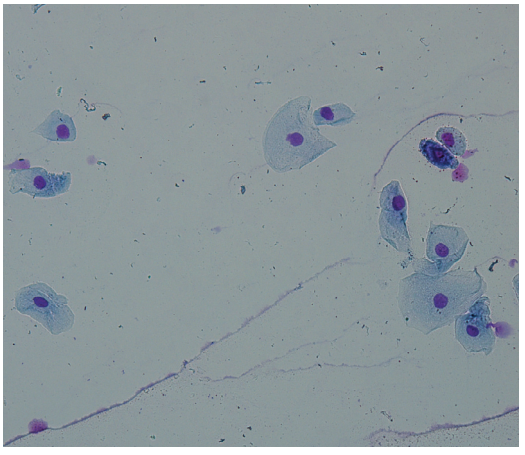

Figure 7 Vaginal cytology of a queen in the interestrus phase of the cycle. Some cells are cornified but make up <50% of all cells and the nuclei are not pyknotic. The remaining cells are smaller with less cytoplasm (intermediate and parabasal cells)

Diestrus

If ovulation occurs (see box), the queen will then enter the diestrus phase. The presence of one or more corpora lutea on the ovary confirms diestrus (Figure 8). The vaginal cytology will change to primarily small intermediate and parabasal cells (Figure 9). Verstegen et al demonstrated that progesterone, secreted by the corpora lutea, begins to rise by day 4 after the first mating and the queen enters a luteal phase.[12] The luteal phase is the period of time where active corpora lutea are located on the ovaries and the queen is exposed to elevated progesterone.

Ovulation

Ovulation is strongly dependent on the number of matings in a short period of time. Wildt et al showed that only 1/12 cats ovulated after a single mating on day 1 of estrus, whereas 4/12 ovulated after a single mating on day 4 of estrus.[11] In contrast, when multiple matings (three) on a single day were allowed, 10/12 cats ovulated on days 1–3 of the estrus period.[11] It is generally recommended that four or more matings are needed to provide sufficient stimulation and release of luteinizing hormone (LH) for ovulation to occur. The LH surge occurs very shortly after mating, peaking at 2 h and remaining elevated until approximately 8–12 h.[1] Ovulation occurs within 36 h of mating, provided preovulatory follicles are present.

Four or more matings are needed to provide sufficient stimulation and release of LH for ovulation to occur.

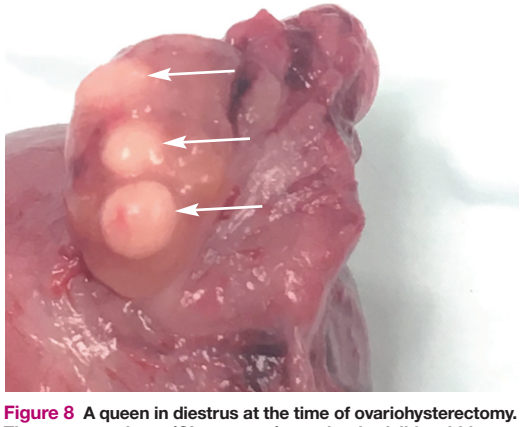

Figure 8 A queen in diestrus at the time of ovariohysterectomy. Three corpora lutea (CLs; arrows) are clearly visible within the ovary. Additional CLs were observed on the other ovary of this queen

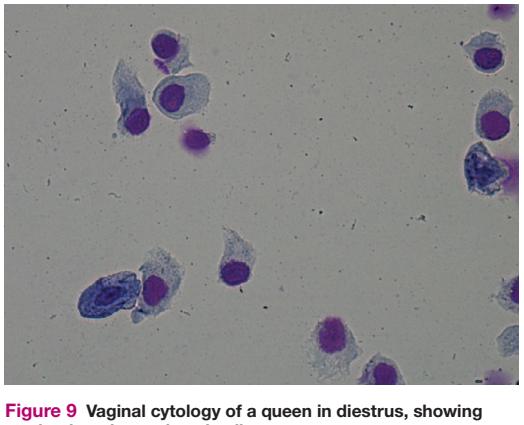

Figure 9 Vaginal cytology of a queen in diestrus, showing predominantly parabasal cells

Mating with a sterile or subfertile tom will negatively affect a breeding program because, once ovulation occurs, the queen will not show another estrus for 40–50 days.

Progesterone and pregnancy

In pregnancy, progesterone has been shown to peak between days 13 and 21 and then gradually decline, reaching baseline by 65 days after mating.[12] The average gestation in the same study was 64 days after the first mating,[12] but it can be highly variable and range from 52–74 days.[13] Ovarian progesterone production is fundamental for pregnancy maintenance in queens.[12] However, the feline placenta has steroidogenic properties, as demonstrated by the fact that ovariectomy during the second half of pregnancy may be followed in some queens by normal parturition at term.[14,15]

Pseudopregnancy

If the queen is mated and ovulates, but does not become pregnant, this leads to pseudopregnancy. This stage lasts approximately 40–45 days, which is shorter than the gestational length of a pregnant queen. With pseudopregnancy, the progesterone increases and peaks as with pregnant queens, but steadily declines after day 30 until it reaches baseline at around 40–41 days after the first mating.[12] The average time to the next estrus following the decline of progesterone is 17 days ± 4 days.[12] Mating with a sterile or subfertile tom can result in prolonged exposure to progesterone because the tom will mate and induce ovulation, and the queen will enter a luteal phase but will not become pregnant. This negatively affects a breeding program because once ovulation occurs, the queen will not show another estrus for 40–50 days. Additionally, exposure to prolonged periods of progesterone can lead to uterine pathology, which further affects fertility.

The length of the non-receptive period of the queen can be used to determine if a queen is ovulating. If the interval of time between estrous (heat) behavior is 10 days, the queen failed to ovulate. If this period is 40–50 days, the queen did ovulate but failed to become pregnant. Testing for serum progesterone 5–7 days after mating will also determine if the queen has ovulated. Progesterone will be low (<2.0 ng/ml) if the queen failed to ovulate, but elevated (>2.0 ng/ml) if the queen did ovulate.

General cattery management

Appropriate breeding management is the key to good fertility in a cattery. Minor changes in procedures may have a significant impact on pregnancy rate and litter size. Management protocols may differ for a private breeding operation, a research colony or a single cat in a household. A detailed history and on-site visit to the cattery or single-cat household will help the veterinarian and owner identify management problems that could affect feline health and fertility. A list of questions to ask can be found in the box.

Prior to breeding, all animals should be up to date on vaccinations, deworming and other preventive healthcare. Vaccinations should be avoided during breeding and pregnancy and should be administered at least 2–3 weeks before mating and subsequent pregnancy is desired. Strict sanitation is essential to prevent spread of disease. Recommendations for sanitation should be made based on animal density, type of housing (carpet vs tile floor) and the disease status of the cattery. Litter boxes and food and water bowls should be sanitized at least weekly for the breeding animals, and more often in the nursery. Cats should ideally be separated based on their breeding status; pregnant queens housed together, non-pregnant queens separated from pregnant animals, and lactating queens with young kittens separated from all other animals. This policy will help prevent the spread of disease from one group to another.

Specific questions to gain a baseline knowledge of cattery management

- How many cats are housed in the facility (male and female, breeding and non-breeding)?
- What are their ages?
- What is the source of each cat and how long has each been with the colony?
- What is the diet, water source and preventive health policy?
- Is there a supplemental lighting program?
- What is the current disinfection policy for floors, litter boxes, bowls, etc?
- What is the procedure for bringing the male and female together?
- Is there a procedure for pregnancy confirmation?
- Where are pregnant queens housed during gestation, birthing (queening) and lactation?
- What bedding or boxes are being provided to the cats at each stage (mating, gestation, queening, lactation)?
- Is breeding or queening observed or does it occur with no one present?
- How are the kittens managed from birth to weaning?
- Can a detailed breeding and queening report for each animal be provided?
- What are the specific issues the cattery is experiencing?

Written records for each queen should be as detailed as possible and include all dates of breeding, observed matings, observations of behavior when with the male, pregnancy diagnosis, queening date, litter size and any other information that may be relevant. Records should also include details of any illness, injuries or breeding problems. Because fertility declines as the queen ages (see 'Breeding management'), the age of the queens should be monitored closely as part of overall management.

Before future breedings are planned, further considerations should be made as to the condition of the queen following pregnancy and lactation, overall health of the queen and the kittens, and any extenuating circumstances surrounding the queen, pregnancy and delivery, and lactation/weaning.

Breeding frequency

For registered cats, the Governing Council of the Cat Fancy (GCCF) advises a minimum of 26 weeks between litters and no more than three litters over 2 years. If a queen has had three or more litters in her lifetime, a maximum of one litter per year thereafter is advised. Exceptions to this rule can be made in cases where the health of the female would benefit from breeding, such as post-pyometra treatment or loss of body condition due to continuous estrus. Such exceptions should be supported by a letter from the primary veterinarian. Purebred queens registered with the GCCF should be designated an 'Active Breeder', which states they are fit to be used as a breeding animal and are free from medical and genetic conditions.

Breeding management

Queens should be at least 12–15 months old before they are allowed to breed and carry their first litter. In this author's experience, fertility begins to decline as early as 3.5–4 years of age and can be severely affected by 5 years. Adequate breeding records should be kept to identify any evidence of subfertility, such as lower litter sizes, increased stillbirths delivered or missed matings (ovulating but not getting pregnant despite adequate mating). Some queens will continue to produce litters well into their lifetime (age 8–10 years), but the risk of complications increases with age. Retirement from breeding should be considered around the age of 6 years for most queens. Analyzing records of previous fertility and litter size will allow appropriate management decisions to be made.

When breeding naturally in a cattery, the queen should be taken to the tom's location, as establishment of a territory is important for the male. The queen should be exposed to the tom when she is showing signs of heat (discussed earlier in the section on 'Estrus [follicular phase]'). Estrus can also be confirmed using vaginal cytology (see box above). When in estrus, the queen can be placed with the male for 1–2 days to allow mating to occur. Separating after this short period of time allows a more accurate queening date. It is important to monitor breeding activity to make sure it is occurring. If heat detection is not possible in a natural mating situation, the queen can be placed with the male for an extended period (usually at least 2 weeks). The pair should be monitored closely for breeding activity or fighting (if the queen is not in estrus). If fighting occurs, the pair should be separated for a few days before retrying, or until the vaginal cytology indicates estrus.

Once the pair has been together, a serum progesterone concentration >2 ng/ml 3–4 days after mating can be used to confirm ovulation. The queen can then be returned to her housing. If the progesterone concentration is <2 ng/ml, mating has likely not occurred, matings were insufficient to induce the LH surge and ovulation, or the queen was still in early estrus and the follicles present were not mature enough to ovulate. The queen should be returned to the male and monitored for breeding activity. Allowing the male access to the female for a longer period of time gives her greater opportunity for breeding but it is more difficult in this scenario to accurately time ovulation and therefore predict the exact due date.

While some queens will continue to produce litters up until 8–10 years of age, retirement from breeding should be considered at around 6 years of age, especially for those showing subfertility or reduced litter size.

Obtaining a vaginal swab

A sample for vaginal cytology can be collected by inserting a moist cotton-tipped swab into the vulva (approximately 1 cm; ie, just the cotton tip), twisting it 1–2 times and then removing it (Figure 10). When performed correctly, a vaginal swab procedure does not provide enough stimulation to induce an LH surge.

Figure 10 Vaginal cytology in a sedated queen. The moistened cotton swab is inserted into the vulva approximately 1 cm (just the cotton tip). The swab is rotated 1–2 times and then removed. The sample should be rolled evenly onto a clean slide and stained with Diff-Quik for evaluation. This procedure is tolerated well by most domestic cats that are in heat, and can usually be performed without sedation

When mating, the tom will scruff the back of the queen's neck with his teeth. The female will assume a crouched position with her hind end elevated (Figure 11) and tail to the side, and will also often tread with her hind feet. The male will use his body to hold the female in place and will make several thrusts. Toward the end of the mating, the penis enters the vulva, ejaculation occurs and semen is deposited into the cranial vestibule. Intromission lasts only a few seconds, and the queen will emit a low growl followed by a yowl in response to the penile spines. Once complete, the female and male separate and the female shows an 'after reaction', involving rolling, rubbing on objects and licking the vulvar area. This post-mating behavior helps confirm that intromission took place. If this behavior is not seen, it is likely that the tom did not achieve intromission.

Figure 11 This is the typical estrus posture, with crouched front legs and elevated hind end. The queen was displaying in front of the cage of an intact male and was also treading with her hind legs

'After reaction' behaviors in the queen, including rolling, rubbing on objects and licking the vulvar area, help to confirm that intromission took place.

Conflict of interest

The author declared no potential conflicts of interest with respect to the research, authorship and/or publication of this article.

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Ethical approval

This work did not involve the use of animals and therefore ethical approval was not specifically required for publication in *JFMS*.

Informed consent

This work did not involve the use of animals (including cadavers) and therefore informed consent was not required. No animals or people are identifiable within this publication, and therefore additional informed consent for publication was not required.

KEY POINTS

- A veterinarian must have an idea of normal feline reproduction before problems can be identified.
- Many problems of reproduction can be due to improper management in the cattery or with the animals themselves.
- In order to solve any problems with breeding, a detailed history of the queen, cyclicity, breeding behavior and living conditions is essential.

References

1 Tsutsui T and Stabenfeldt GH. **Biology of ovarian cycles, pregnancy and pseudopregnancy in the domestic cat.** *J Reprod Fertil Suppl* 1993; 47: 29–35.

2 Roberts SJ. Veterinary obstetrics and genital diseases (theriogenology). 3rd ed. Woodstock, VT: Literary Licensing, 1986.

3 Watson PF and Glover TE. **Vaginal anatomy of the domestic cat (*Felis catus*) in relation to copulation and artificial insemination.** *J Reprod Fertil Suppl* 1993; 47: 355–359.

4 Del Campo CH and Ginther OJ. **Arteries and veins of uterus and ovaries in dogs and cats.** *Am J Vet Res* 1974; 35: 409–415.

5 Gatel L, Rault DN, Chalvet-Monfray K, et al. **Ultrasonography of the normal reproductive tract of the female domestic cat.** *Theriogenology* 2020; 142: 328–337.

6 Zambelli D and Cunto M. **Vaginal and cervical modifications during the estrus cycle in the domestic cat.** *Theriogenology* 2005; 64: 679–684.

7 Leyva H, Madley T and Stabenfeldt GH. **Effect of light manipulation on ovarian activity and melatonin and prolactin secretion in the domestic cat.** *J Reprod Fertil Suppl* 1989; 39: 125–133.

8 Binder C, Aurich C, Reifinger M, et al. **Spontaneous ovulation in cats – uterine findings and correlations with animal weight and age.** *Anim Reprod Sci* 2019; 209. DOI: 10.1016/j.anireprosci.2019.106167.

9 Gudermuth DF, Newton L, Daels P, et al. **Incidence of spontaneous ovulation in young, group-housed cats based on serum and faecal concentrations of progesterone.** *J Reprod Fertil Suppl* 1997; 51: 177–184.

10 Shille VM, Lundstrom KE and Stabenfeldt GH. **Follicular function in the domestic cat as determined by estradiol-17 beta concentrations in plasma: relation to estrous behavior and cornification of exfoliated vaginal epithelium.** *Biol Reprod* 1979; 21: 953–963.

11 Wildt DE, Seager SW and Chakraborty PK. **Effect of copulatory stimuli on incidence of ovulation and on serum luteinizing hormone in the cat.** *Endocrinology* 1980; 107: 1212–1217.

12 Verstegen JP, Onclin K, Silva LD, et al. **Regulation of progesterone during pregnancy in the cat: studies on the roles of corpora lutea, placenta and prolactin secretion.** *J Reprod Fertil Suppl* 1993; 47: 165–173.

13 Root Kustritz MV. **Clinical management of pregnancy in cats.** *Theriogenology* 2006; 66: 145–150.

14 Tsutsui T, Suzuki Y, Toyonaga M, et al. **The role of the ovary for the maintenance of pregnancy in cats.** *Reprod Domest Anim* 2009; 44: 120–124.

15 Siemieniuch MJ, Jursza E, Szostek AZ, et al. **Steroidogenic capacity of the placenta as a supplemental source of progesterone during pregnancy in domestic cats.** *Reprod Biol Endocrinol* 2012; 10: 89. DOI: 10.1186/1477-7827-10-89.