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Article #1 (1.5 contact hours)
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KEY FACTS

- When allowed to mate naturally, queens easily bear 50 to 100 kittens in a breeding life.
- Lactation may not suppress estrus in cats, and many queens become pregnant while nursing their young.
- Relaxin is the only pregnancy-specific hormone in cats and can be used to diagnose pregnancy.

Prolific Cats: The Estrous Cycle*

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ABSTRACT: The estrous cycle of the female cat (queen) is unique among domestic species and consists of five phases: proestrus, estrus, interestrus, diestrus, and anestrus. A broad range of individual variation in cycle length exists among queens. Female cats are seasonally polyestrous, extremely fertile, and precocious. Ovulation may be induced by both copulatory and noncopulatory stimulation. Pregnancy may be diagnosed by physical examination, radiography, ultrasonography, and measurement of plasma relaxin concentrations.

The reproductive cycle of the domestic queen (female cat) is unique. Like female rabbits, queens are capable of multiple pregnancies within a single reproductive season, making them one of the most prolific domestic species. This article reviews the normal reproductive physiology and behavior of the queen.

PUBERTY

On average, queens reach puberty or experience their first estrous cycle between 5 and 9 months of age, although the onset may range from 3.5 to 18 months.¹ In addition to age, factors that affect the onset of puberty include breed, time of year or photoperiod, social environment, health, physical condition, and nutritional plane.^{1,2} With adequate physical and nutritional status, adolescent queens may begin to cycle after attaining a body weight of approximately 2 kg.²

In the Northern Hemisphere, queens start to cycle in late January and February as the days get longer (i.e., the photoperiod increases). Therefore, kittens born during the previous spring and summer months frequently reach puberty at similar times despite age differences, provided they are of adequate weight and body condition. Free-roaming queens often cycle earlier than housecats.^{2,3} Group housing or the introduction of a tomcat or a queen in estrus provides social stimuli that hasten the onset of estrus.^{4,5}

Breed also affects onset of estrus.¹ In general, domestic shorthair cats reach puberty earlier than do domestic longhair cats, and mixed breeds reach puberty earlier than do purebreds. In particular, Persians are notoriously late in reaching sexual maturity, frequently not cycling until 12 months of age. On the other

*A companion article entitled "Prolific Cats: The Impact of Their Fertility on the Welfare of the Species" appears on page 1058.

hand, Burmese queens frequently cycle as early as 3.5 to 4.5 months of age.

SEASONALITY

Free-roaming queens are seasonally polyestrous. In the Northern Hemisphere, the season begins in January or February (after the winter solstice, as the days get longer) and lasts until fall. The season for an average queen begins in February and ends in late September.² Anestrus persists from October through December until the new season begins in January or February. A few queens, particularly those living in warm climates, may continue to cycle as late as November before entering a brief anestrus period.

On average, queens display estrous behavior every 2 weeks during the season unless one of the following occurs:

- Pregnancy
- Pseudopregnancy (ovulation without fertilization)
- Sterilization
- Serious illness

The peak season is February to March and May to June (which shifts to July to August in northern, temperate climates).²

In contrast to free-roaming cats, indoor cats may be influenced by artificial lighting. In an environmentally controlled laboratory setting, 10 or more hours of light in a 24-hour period are required for reproductive cycling and allow queens to cycle throughout the year.⁶ Maintaining a 14-hour photoperiod and the use of natural-daylight spectrum fluorescent bulbs assures a maximum fertility period and estrous cycling.⁷ Estrous cycling typically occurs within 7 to 10 weeks of instituting such a light cycle^{8,9}; however, this period can be shortened if preceded by a nonstimulatory light cycle of 8 or fewer hours of light^{5,10} or if a tomcat or queen in estrus is introduced at the time that the duration of light is increased.^{4,5}

Although this response is predictable in a controlled laboratory setting, it is less predictable in a home environment because light patterns are rarely constant. The vast majority of housecats experience winter anestrus.² Siamese queens appear less sensitive to photoperiod than do other breeds and tend to cycle year-round.¹ In contrast, longhaired cats are more sensitive to photoperiod and winter estrus in these cats is rare.⁶

FERTILITY

The domestic queen has long been recognized for her fertility (Figure 1). In ancient Egypt, she was



Figure 1—Domestic queens are excellent as well as prolific mothers, producing an average of two to three litters per year if allowed to breed uncontrolled.

worshipped as a symbol of fertility. In fact, the Egyptian goddess of fertility, Bastet, was portrayed as a cat. Extreme examples of the domestic queen's fertility exist in the literature, including a report of a 26-year-old queen successfully delivering kittens.¹¹ Another queen delivered a litter consisting of 19 kittens.¹²

Peak reproductive activity occurs between 1.5 and 8 years of age, with an average of two to three litters per year and three to four kittens per litter (range, 1 to 15 kittens per litter).² Queens easily bear 50 to 150 kittens in a breeding life of approximately 10 years if allowed to mate naturally. Adolescent queens (younger than 1 year of age) and queens older than 8 years of age tend to cycle irregularly and have smaller litters, more abortions, and more stillbirths.² Despite their lack of optimal reproductive performance, however, adolescent queens and queens older than 8 years of age commonly have successful pregnancies.

Like tomcats, queens are polygamous and rarely form long-term bonds with a mate, although they often display preferences for particular partners.^{5,13} If allowed, a female may accept several males during the estrous period and therefore litters may have multiple sires (a phenomenon termed *superfecundity*).

After normal lactation and weaning, queens return to estrus in 2 to 8 weeks (average, 4 weeks).² In many queens, lactation does not suppress estrus and a return to fertile cycling is seen during the second to fifth week of lactation.¹⁴ If a queen aborts or if the litter is taken away within 3 days of parturition, she will return to estrus in approximately 1 week.² Some queens experience estrus during pregnancy. In fact, 10% of female cats experience estrus between the third and sixth weeks of pregnancy.¹ Fertile cycles are rare in pregnant queens, but the development of fetuses of different ages

resulting from separate matings in different estrous cycles (known as *superfetation*) can occur.¹

ESTROUS CYCLE

The feline estrous cycle consists of five phases: proestrus, estrus, interestrus, diestrus, and anestrus (Table 1).

Proestrus

Proestrus is the first phase and is the time during which queens attract toms but are not sexually receptive to them. Rapid ovarian follicular growth and estradiol synthesis occur during this phase. Queens typically vocalize; rub their faces against objects, other cats, or human companions; and act “friendly.” Rubbing usually progresses to rolling, and many queens stretch and squirm in lateral recumbency, opening and closing their paws. Queens may assume a lordosis stance and tread in place with their hindlimbs. Upon introduction to a tomcat, however, they will not be sexually receptive and may aggressively turn on the male, hissing and striking out with their claws.

Proestrus can last from 12 hours to 3 days.^{2,14,15} Signs may be overt or subtle—in fact, proestrus is not observed regularly in all queens. Many queens shift abruptly from no display of sexual behavior to standing, receptive heat.

Estrus

Estrus is the phase of sexual receptivity that lasts an average of 4 to 7 days, with a range of 1 to 21 days.^{2,14–17} During this period, serum estradiol concentrations rise sharply. Under the influence of estradiol,

the labia of the queen’s vulva become slightly edematous and hyperemic but remain small and well covered by hair, requiring close inspection to identify changes. Vulvar discharge is scant and, because of the fastidious grooming habits of queens, rarely observed.

During estrus, queens commonly vocalize and call to toms when approached. They crouch and posture in a lordosis stance, treading in place with their hindlimbs. In this position, the queen’s ventral thorax and abdomen touch the floor, her perineum is elevated, and her tail is deflected laterally as she presents herself to her mate. This stance can usually be induced by stroking the queen’s back or dorsal rump during estrus. Occasionally, estrual queens exhibit urine spraying and marking.²

Interestrus

Because cats are polyestrous and do not ovulate after every estrus phase, an interestrus period (or nonestrous interval) commonly follows estrus. Interestrus is the interval of sexual inactivity between waves of follicular function in cycling queens. During this period, serum estradiol concentrations rapidly return to basal levels and all breeding behaviors cease. Queens typically return to proestrus within 1 to 3 weeks, although the length of this period varies and may range from 3 days to 7 weeks.^{2,14–17}

Diestrus

If ovulation occurs during estrus, diestrus follows. Corpora lutea form within 24 to 48 hours of ovulation and begin secreting progesterone.² They remain functional for 30 to 50 days (average 35 days) in

Table 1. The Estrous Cycle of the Domestic Cat

	<i>Proestrus</i>	<i>Estrus</i>	<i>Interestrus</i>	<i>Diestrus</i>	<i>Anestrus</i>
Duration	0.5–3 days	Average: 4–7 days Range: 1–21 days	Average: 1–3 weeks Range: 3 days–7 weeks	Average: 35 days Range: 30–50 days (luteal function)	October/November– January/February (free-roaming cats)
Signs	Rubbing and rolling Affectionate behavior Lordosis Treading Not receptive to tomcats Vocalization	Sexually receptive Lordosis Treading Tail deflection Vocalization	None	None; breeding activity ceases for 30–100 days (average 45–50 days)	None
Hormone Activity	Ovarian follicular growth and estradiol synthesis	Follicular phase; sharp increase in estradiol concentrations	Baseline estradiol and progesterone concentrations	Formation of corpora lutea; progesterone dominant phase	Baseline estradiol and progesterone concentrations

nonpregnant queens, at which time regression occurs. An interestrus interval follows, such that diestrus queens cease breeding activity for 35 to 100 days (average 45 to 50 days) before proestrus/estrus resumes.^{16,18} Because breeding activity ceases during this phase, it is behaviorally indistinguishable from anestrus or interestrus.

On rare occasions, queens exhibit behavioral signs of estrus at the conclusion of diestrus as progesterone concentrations decline to basal levels.⁵ In such cases, hormonal estrus is absent and estradiol concentrations remain at basal levels.⁵

Anestrus

Anestrus is the period of sexual rest that occurs between October and January in most free-roaming queens. Anestrus queens are sexually noninviting and nonreceptive. They may hiss or strike out at toms making sexual advances.

BREEDING BEHAVIOR

Courtship usually occurs at night. Receptive queens sit at a distance from competing males and crouch, roll, and tread in place. Fighting may occur between males as they mark out territories surrounding females. Vocalization is not limited to fighting and is more often associated with courtship and mating. Queens utter low monotone howls known as heat cries, while males caterwaul in response, signaling their readiness to mate.¹ A male may approach a receptive female and rub chins and faces with her before mating. Courtship lasts from 10 seconds to 5 minutes, and the duration decreases with repeated breedings.¹ Mating is accomplished as the tom grasps the female by the neck with his teeth, grips her forequarters with his front legs, and straddles her with his hindlimbs. Intromission and ejaculation occur within a few seconds (Figure 2).

After the tom releases his grip, he rapidly retreats as the female displays a postcoital "after-reaction," which lasts up to several minutes. The after-reaction is characterized by a loud scream (the copulatory scream), followed immediately by vigorous rubbing and rolling on the ground or floor and licking of the vulva.¹ During this time, the queen is unreceptive to the male and if he approaches, she will strike out at him. Additional matings, with the same or different tomcats, usually resume within 20 to 30 minutes.¹ Several matings (10 to 30) commonly occur during the next 24 hours and continue over several days with the interval between matings becoming increasingly longer.¹ Coital contact does not shorten the queen's period of receptivity.^{2,17}

An after-reaction may occur in some estrual queens following mechanical stimulation, such as petting



Figure 2A



Figure 2B



Figure 2C

Figure 2—Mating sequence of the domestic cat. (A) An interested male approaches a queen in estrus. (B) As the tom prepares to grasp her neck, the queen exhibits lordosis and tail deflection. (C) The tom mounts the queen. Intromission and ejaculation occur within 5 to 15 seconds.

down the back or scratching the dorsal rump. Owners can be quite alarmed by this behavior, often confusing it with a seizure. Similarly, owners may not recognize normal estrous behaviors and may mistake excessive lordosis and treading for seizure activity in their cats.

OVULATION AND PSEUDOPREGNANCY

The domestic cat is an induced ovulator. Until recently, queens were believed to require copulation or direct mechanical stimulation of the vagina and cervix to ovulate. Release of luteinizing hormone (LH) from the anterior pituitary occurs within minutes of copulation in cats, with subsequent ovulation occurring in 30 to 50 hours.¹⁹ A linear relationship exists between the number of sexual contacts, the magnitude and duration of LH release, and the likelihood of successful ovulation.¹⁸

Ovulation induced by noncopulatory stimulation can also occur in cats and is much more common than previously believed. Numerous studies have demonstrated progesterone concentrations consistent with ovulation in nonbred queens.^{5,16,19,20} Luteal phase diseases, including feline inflammatory uterine disease and pyometra, occur in individually housed or nonbred queens.^{16,21} Types of noncopulatory stimulation that induce ovulation may include the stroke of a hand down the back; other physical stimulation; or visual, auditory, or olfactory cues from a nearby tomcat.^{16,19,22}

Pseudopregnancy occurs when a queen ovulates but does not become pregnant. Corpora lutea develop as a result of ovulation and synthesize and secrete progesterone. Progesterone inhibits secretion of gonadotropin-releasing hormone from the hypothalamus and hence LH and follicle-stimulating hormone from the anterior pituitary. The pseudopregnant queen does not exhibit estrus while under the influence of progesterone. She ceases breeding behavior for 35 to 100 days (average 45 to 50 days).^{2,16} Cats differ from bitches and other carnivores in that the luteal phase of nonpregnant queens is only half as long as gestation, allowing a more rapid return to a fertile state.² In addition, clinical signs of pseudopregnancy (pseudocyesis) are very rare in cats. When present, they are usually mild but may include lactation, nesting, and tending kittens.²

PREGNANCY

In free-roaming queens, there is a bimodal incidence of pregnancy: Most kittens are born in midspring and late summer.³ Some queens have a third litter in late fall. The queen's gestation period is 65 to 67 days on average, with a range of 62 to 71 days.¹⁷ Gestation length is variable due to the relatively long period of

sexual receptivity and the uncertainty of the time of ovulation and conception. The gestation period may be divided into three trimesters, each approximately 3 weeks in duration.

Pregnant cats should be allowed moderate exercise and should be fed a high-quality feline diet designed for growth or lactation. Caloric intake increases by approximately one third by midgestation.²³ Stress should be avoided in pregnant queens and a quiet, warm, dark nesting area should be provided during the last trimester.

PREGNANCY DIAGNOSIS

Behavioral and physical changes may aid in pregnancy diagnosis, but such changes are typically subtle during the first two trimesters. Many queens become increasingly docile during this period and exhibit "pinking" of the nipples (the nipples become pinker and more erect).¹ (Ironically, in the author's experience, cats in the early stages of pregnancy, when physical signs of their condition are lacking, are frequently offered for adoption by humane shelters because of their docile, friendly temperaments.) By the third trimester, behavioral and physical changes are obvious and include abdominal distention, enlargement of the mammary glands, excessive grooming of the mammary and perineal areas, and nesting behavior (Figure 3).

Relaxin is the only pregnancy-specific hormone in cats.²⁴ Pregnancy gonadotropins are not known to exist, and serum progesterone concentrations are not helpful in diagnosing pregnancy because they do not significantly differ in pregnant and pseudopregnant queens.² Plasma relaxin assays (Witness[®] Relaxin, Synbiotics Corp, San Diego, CA) may be used to diagnose pregnancy in dogs after day 22 to 24 of pregnancy.²⁵



Figure 3—Although physical changes remain subtle during the first two trimesters of pregnancy, they become obvious after the sixth or seventh week. Note the abdominal distention and mammary development.

and may become available for use in cats. Preliminary data suggest that this assay is useful after 26 to 28 days of pregnancy in cats.²⁶ Relaxin is secreted by the placenta. Plasma relaxin concentrations increase from days 20 to 30 after mating and remain elevated throughout pregnancy and for the first few days after birth. The luteotrophic effects of relaxin help to maintain pregnancy and result in relaxation or softening of the connective tissues of the pelvis.²⁴

Abdominal palpation is the most common method for diagnosing pregnancy in queens.² Fetuses may first be palpated at day 17 (2.5 weeks of gestation) as discrete, firm, spherical nodules that are 2 to 2.5 cm in diameter. By day 25 (3.5 weeks of gestation), fetuses are no longer discretely palpable. Instead, generalized uteromegaly is evident and remains palpable through parturition. By week 7 of gestation, fetal heads can be palpated. With experience, palpation is very reliable for detecting pregnancy and is the most economical and practical method.²⁷

Imaging methods used for pregnancy diagnosis include radiography and ultrasonography. Calcification of the fetal skeletons may occur as early as day 38 of gestation but is not a reliable finding until day 43. Therefore, to ensure diagnostic results, radiography should be performed after day 43 of gestation.² Uteromegaly may be seen before this time but cannot be distinguished from pyometra or other inflammatory uterine diseases. Abdominal radiographs are most useful for evaluating litter size before parturition. Ultrasonography is rapid, safe, and reliable for pregnancy detection in cats. Ultrasonographic evidence of pregnancy may be seen as early as 11 to 14 days, and fetal heartbeats can be recognized at 3.5 to 4 weeks of gestation.²⁸

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ARTICLE #1 CE TEST

The article you have read qualifies for 1.5 contact hours of Continuing Education Credit from the Auburn University College of Veterinary Medicine. Choose the best answer to each of the following questions; then mark your answers on the postage-paid envelope inserted in *Compendium*.

1. On average, queens reach puberty at what age?
 - a. 3 to 6 months
 - b. 5 to 9 months
 - c. 1 year
 - d. 18 months
 - e. 2 years
2. Queens are seasonally polyestrous. The season usually begins and ends, respectively, in which of the following months?
 - a. January, August
 - b. February, September
 - c. early March, late October
 - d. late September, early March to April
 - e. April to May, October
3. Queens
 - a. may experience estrus during pregnancy.
 - b. may experience estrus while lactating.
 - c. are not likely to become pregnant if they are younger than 14 months of age.
 - d. a and b
 - e. none of the above
4. In queens, estrus
 - a. is the phase of sexual receptivity.
 - b. lasts an average of 4 to 7 days.
 - c. is usually followed by the interestrous interval if pregnancy does not occur.
 - d. is occasionally associated with urine spraying.
 - e. all of the above
5. The after-reaction
 - a. occurs following mating and shortens the queen's period of receptivity.

- b. occurs following diestrus and indicates a return to estrus.
 - c. is characterized by a loud scream, vigorous rubbing, rolling, and licking of the vulva.
 - d. is associated with successful ovulation.
 - e. a and c
6. Which of the following statements regarding ovulation in cats is true?
- a. Cats are induced ovulators.
 - b. Cats are spontaneous ovulators.
 - c. Progesterone concentrations increase after ovulation.
 - d. Both copulatory and noncopulatory stimuli may induce ovulation in cats.
 - e. a, c, and d
7. The luteal phase of cats
- a. is characterized by increased serum progesterone concentrations.
 - b. is frequently associated with pseudocyesis.
 - c. is commonly associated with estrous behavior, including lordosis and treading.
 - d. results in cessation of breeding behavior for an average of 45 to 50 days.
 - e. a and d
8. The normal gestation period of cats averages _____ days.
- a. 45 to 48
 - b. 58 to 60
 - c. 65 to 67
 - d. 72 to 75
 - e. 77 to 79
9. The hormone relaxin
- a. is a pregnancy gonadotropin found in feline urine.
 - b. is as reliable as serum progesterone for diagnosing pregnancy in cats.
 - c. is the only pregnancy-specific hormone in cats.
 - d. a and b
 - e. a and c
10. Which of the following statements regarding pregnancy diagnosis in cats is true?
- a. Fetuses can first be palpated at approximately 2.5 weeks of gestation.
 - b. Calcification of fetal skeletons occurs by day 43, after which time radiographs are useful for pregnancy diagnosis.
 - c. Ultrasonography is a reliable method of pregnancy detection in cats.
 - d. b and c
 - e. all of the above
-