

Reproductive behavior of small animals

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Abstract

Normal and abnormal reproductive behavior of dogs and cats, and known and proposed hormonal bases for these behaviors are addressed. Emerging information includes use of oxytocin to promote pair-bonding between dam and offspring and the possible effect of prolactin in inhibiting sexual behaviors.

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1. Introduction

Reproductive behavior has been well described in most species, but the underlying physiologic basis of sexual behavior has not received the same attention. An understanding of information from laboratory animal species and research in humans may promote differing approaches to diagnosis and treatment of abnormalities of reproductive behavior in dogs and cats.

2. Endocrinology

Oxytocin is a peptide hormone, released from the posterior pituitary, secondary to neurologic stimulation. The two stimuli best documented to cause oxytocin release are pressure of the head of a puppy into the cervix during whelping (Ferguson's reflex) and suckling of the mammary glands by the pups. In both instances, nerve cells in the

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hypothalamus that produce oxytocin are stimulated to fire. During breeding, oxytocin may cause smooth muscle contractions in the female's reproductive tract, improving movement of spermatozoa to the site of fertilization. Oxytocin causes synchronized contractions of the uterus during parturition and contributes to further dilation of the cervix. During lactation, oxytocin stimulates letdown of milk into the mammary glands. Blood oxytocin concentrations are high in dams while they are nursing. The quantity of oxytocin secreted may be correlated with efficiency of milk production in some species [1]. Oxytocin also has been associated with increased sexual receptivity in some species and may be involved in formation of the normal pair-bond between dams and offspring [2].

Prolactin is a protein hormone that induces milk production and stimulates normal maternal behavior. Its production is stimulated during pregnancy and concentrations of prolactin in blood rise sharply at the time of whelping, as other hormone concentrations abruptly decrease. Hyperprolactinemia has been associated with abnormal reproductive behavior and function in humans [3]. Prolactin also may be involved in the refractory period exhibited by most animals for a time after mating; in humans, prolactin concentrations in blood increase after orgasm [4].

Estrogen, produced from the granulosa cells of the ovary, causes the physical and behavioral changes we associate with estrus in dogs, including vulvar swelling, exudation of serosanguinous vulvar discharge, and attraction of male dogs [5,6]. The predominant estrogen secreted in dogs is estradiol-17 β . There are two types of estrogen receptors, named estrogen receptor α (ER α) and ER β . Distribution of these receptors within the brain varies, presumably because activation of these receptors elicits different behaviors [7]. Concentration of estrogen receptors in the brain also varies with physiologic status of the animal; fasted animals had a decline in receptor number and a decline in mating behavior [8,9]. Estrogen may stimulate genes for production of opioids and oxytocin; these are thought to provide mild pain relief and to decrease anxiety. This may be what allows a female to stand to be bred when such contact usually would be considered an attack. Finally, naturally occurring products in plants that activate estrogen receptors, phytoestrogens, may be associated with irregular estrous cycles in some species [10].

After ovulation, the corpora lutea secrete progesterone. Progesterone is responsible for pregnancy maintenance and to that end, it promotes secretion of intrauterine glands to support the fertilized eggs, stimulates development of the mammary glands, and induces maternal behavior. Secretion and effect of progesterone are complex, also involving co-activator proteins and brain chemicals [11]. Progesterone can, in some circumstances, activate oxytocin receptors [12]. Progesterone receptors are activated more quickly if the animal is primed with estrogen. Behavioral effects of excessive progesterone are inhibitory; feral cats receiving an oral progesterone-type compound in food showed fewer estrous cycles, lack of sexual interest and loss of "social status" [13]. These changes probably are due to negative feedback of progesterone to the hypothalamus and pituitary, decreasing pulsatile release of GnRH and FSH. Abrupt decline in progesterone concentrations and a subsequent rise in prolactin cause many of the normal mothering behaviors seen in dogs, including nesting and maternal aggression. Loss of progesterone at birth is thought to be part of the complex causing "the baby blues" in women.

During embryonic development, the testes secrete Mullerian inhibiting factor, which prevents development of the female tubular reproductive tract, and testosterone, which

stimulates development of the male tubular reproductive tract. Continuing secretion of testosterone is necessary for continuing spermatogenesis in male dogs. Testosterone and its metabolite, dihydrotestosterone (DHT) are responsible for normal breeding behavior.

Normal male dogs and cats are exposed to significant amounts of testosterone and DHT during development. Normal female dogs and cats are exposed to significant amounts of estrogen. Timing and concentration of testosterone and estrogen exposure must be correct for normal fetal development to occur [14]. Occasionally, a bitch or queen will be exposed to chemicals, including medications and products naturally occurring in plants, which exert a hormonal effect and cause defects in the puppies or kittens.

If the bitch or queen is exposed to testosterone or other androgens during pregnancy, the female offspring will be masculinized. Physical abnormalities of the internal reproductive tract may be present, as may abnormal external genitalia. Severely masculinized females have no vulva or vagina and a clitoris so enlarged as to resemble a penis. These females never show signs of estrus or normal mating behavior. A similar circumstance has been reported to occur in female pups or kittens that lie between two male littermates in the uterus, presumably because the female is exposed to the male siblings' testosterone. However, this effect is unlikely to be significant in the majority of cases because the placentas of puppies and kittens do not connect and there is no transfer of blood directly between them.

Feminization of offspring due to exposure of the dam to estrogen occurs very rarely. Feminization more commonly is associated with abnormalities of chromosome number. Calico (orange, black and white) and tortoiseshell (black and orange) cats provide the best example. The gene controlling the colors black and orange is on the X chromosome. Since male cats should have only one X chromosome (38, XY), they can be black or orange but not both. Male cats demonstrating both colors must have more than one X chromosome (39, XXY or 38, XY/38, XY chimera). These cats usually are infertile and may or may not show normal mating behavior.

Male dogs and cats require exposure to testosterone before and immediately at the time of birth if they are to show normal development and normal reproductive behavior as adults [15]. The exposure to testosterone at birth is a priming effect; animals not exposed to testosterone at birth could not respond to the presence of testosterone at puberty with normal breeding behavior.

Exposure to estrogen at the time of birth may be important for later reproductive success in both males and females [16]. In male laboratory animals, lack of estrogen exposure at birth has been associated with delayed onset of puberty and decreased frequency of mounts when breeding.

Oxytocin is first secreted to a substantial extent in rodents in the early postnatal period. However, experimental administration of oxytocin has been demonstrated to delay puberty onset in female rats [17,18]. The exact role of oxytocin secretion at birth in dogs and cats, if any, is unclear.

3. Pheromones

Pheromones, chemical substances that alter behavior or physiology of another animal through olfaction are an important part of reproductive behavior in animals. Some

Table 1
Pheromone-based effects on murine reproduction

Name of effect	Physiologic and/or behavioral consequence
Bruce effect	Introduction of a male to females pregnant by another male induces pregnancy loss and subsequent return to estrus
Whitten effect	Introduction of a strange male to a group of females induces synchronous estrus
Lee-Boot effect	Females housed in groups exhibit longer estrus periods than do females housed alone
Vandenbergh effect	Juvenile females exposed to males exhibit earlier onset of puberty
Koyama S, 2004	Males exposed to soiled bedding from estrous females have increased density of spermatozoa in their ejaculate

pheromones induce a signaling effect, in which the pheromone induces a behavior change in another animal not associated with a physiologic change. Others induce a primer effect, in which the pheromone induces a physiologic change in another animal [19]. It is assumed, but not proven, that pheromones induce hormonal changes in dogs and cats associated with reproduction. Pheromone effects are well described in the mouse (Table 1). In the dog, the pheromone produced by females identifying her as being in heat has been chemically elucidated (methyl-*p*-hydroxybenzoate) and a commercial product containing this compound marketed for enhancing male libido [20]. An associated compound, methylparaben, often is used as a preservative in shampoos and may be a cause of male dogs exhibiting sexual interest in female dogs that are not in heat. Female dogs housed together eventually will go through heat together (“dormitory effect”). Male dogs identify female dogs as being in heat by investigating the female’s urine, anal gland secretions and vulvar secretions, which presumably contain these products.

4. Sexually dimorphic behaviors

Sexually dimorphic behaviors are those that differ due to gender (Table 2). Be aware that sexually dimorphic behaviors may occasionally be seen in animals of the “wrong” gender in normal circumstances. For example, although male dogs exhibit urine marking more frequently than female dogs in general, intact female dogs are more likely to urinate frequently and to direct urine toward objects when they are away from their home area [21].

Table 2
Sexually dimorphic behaviors of dogs and cats

Behavior	Male	Female
Urine marking (frequent urination, directing urine at objects)	X	
Lifting leg to urinate	X	
Squatting to urinate		X
Urine spraying (vertical surfaces)	X	
Roaming	X	
Mounting other animals, people or inanimate objects	X	
Aggression toward individuals of same gender	X	
Investigation of urine, hindquarters of individuals of opposite gender	X	
Flagging, standing to be bred		X
Nesting and other maternal behaviors		X

Sexually dimorphic behaviors also may vary depending on the location and physiologic state of the animals involved [22]. For example, dispersal of juvenile wild dogs from the territory into which they were born varies with number of animals in the home territory and presence or absence of the parent of the opposite gender [23]. Presumably, this variation helps prevent inbreeding and competition for mating opportunities. Aggression between animals is much more common in males than in females and occurs in both dogs and cats [24–26]. However, when space is not at a premium, dogs show minimal aggression to strange male dogs [27]. Aggressive encounters were much more common when dogs encountered unfamiliar dogs more frequently due to space constraints or when females in heat were present, stimulating competition for mating [28]. The presence of unfamiliar males also is more common when a bitch is in estrus; males have been documented to roam up to 8 km to find a bitch in heat [29].

Castration and ovariectomy (OHE) often are suggested as means to control problem behaviors in dogs and cats. Dogs that have undergone OHE no longer exhibit the behaviors of estrus, which, while normal, are annoying to many owners. OHE is not associated with beneficial changes in behavior, nor is it associated with detrimental changes, except perhaps an increase in indiscriminate appetite [30]. Conversely, allowing bitches to go through one estrus or to be bred before OHE also has not been demonstrated to cause beneficial changes in behavior.

Castration can be an effective technique for controlling some negative behaviors of male dogs and cats. The effect is greatest for sexually dimorphic behaviors, such as urine spraying in male cats, and urine marking, roaming and mounting behaviors in male dogs [31]. Neither the age of the animal nor the duration of time he had exhibited the undesirable behavior prior to castration were correlated with likelihood of resolution [32]. Castration has not been demonstrated to have a significant impact on aggressive behaviors in male dogs, but will decrease intermale aggression in male cats. Finally, castration may be associated with faster progression of age-related cognitive impairment in dogs, suggesting a protective effect of testosterone on brain function at some level [33].

5. Mating behaviors

5.1. Proestrus

Proestrus, the first stage of the estrous cycle, is a time of preparation for fertile breeding. The follicles on the ovaries are maturing to the point where ovulation can occur. The vaginal lining thickens to form a layer of cornified cells, presumably to decrease discomfort for the bitch or queen during breeding. Inexperienced males are interested during this stage, but experienced males often are not. Male dogs determine if a bitch is in heat by licking and sniffing at her urine, anal gland secretions and vulvar secretions [34]. The pheromones in these secretions are pulled into the vomeronasal organ in the mouth and nasal cavity. Some species of animal exhibit “flehmen”, a pulling back of the lips and nostrils that enhances movement of inhaled substances to the olfactory bulb. Male dogs and cats do not exhibit flehmen because their lips are too firmly attached to their upper jaw to allow much movement. Instead, many animals will stand with their head erect and neck

extended for a moment. Frequency of urination of the bitch increases as she progresses through proestrus and oftentimes the male will urinate over the bitch's urine, presumably to "hide" her scent from competing males [29]. Some male dogs are able to determine not just if the bitch is in estrus, but if she is at the optimal time for breeding; presumably this, too, is pheromone-mediated.

Male cats determine if a queen is in heat by sniffing and licking at her perineal area. Investigation of urine is difficult due to the normal, secretory urinary habits of cats and queens do not produce vulvar secretions during proestrus and estrus. Most queens do not go through a discernible proestrus and stand to be bred as soon as the male is interested. The sniffing behavior shown by male dogs and cats is associated with an increase in the concentration of testosterone in their blood.

Estrogen stimulates these physical changes and these behaviors. It has been demonstrated that information from the olfactory area of the brain and from the genitalia stimulates pathways to the spinal cord and the brain, readying the animal for copulation. Estrogen induces development of new neural connections along this pathway [35].

5.2. Estrus

Estrus is standing heat. By its simplest definition, an animal is not in estrus unless they will allow breeding to occur. Female dogs may passively accept the attentions of the male or may show soliciting behavior, consisting of licking at the male, approaching with her perineum exposed or running away ("teasing"). The male dog investigates the female and, if she stands and is not hostile, will attempt to mount. Normal breeding behavior takes practice; 97% of experienced males mount the hindquarters of estrous bitches, while only 39% of inexperienced males mount the bitch at her hindquarters [29]. The amount of time before the male mounts and the number of mounts he attempts before intromission (introduction of the penis into the vagina) occurs is variable and is not associated with fertility. The male dog clasps his forelimbs just in front of the bitch's hindlimbs and thrusts vigorously for several minutes. Spermatozoa are deposited into the vagina at that time. As the male's penis continues to engorge, it becomes too large to be withdrawn from the vagina and the copulatory lock, or tie, is formed. The male, with his penis still within the vagina of the bitch, steps off and lifts one hindleg over her back so the two dogs are standing "butt to butt". The tie usually lasts about 15 min. During this time, the female's vagina is contracting and the male is sending pulses of prostatic fluid down the vagina; these actions promote forward movement of spermatozoa. Most animals stand quietly during the tie but it is recommended that the dogs not be left unattended so neither is damaged by the other walking around. Some bitches show short-lived aggression as the tie is broken, presumably due to pain [36]. Some male dogs that do not achieve a tie will show a "phantom tie", where they stand quietly for a time after breeding and ejaculate prostatic fluid although the penis is not caught within the vulvar lips [29].

It is best to minimize the number of males present when attempting to breed a bitch. If one or two males are present, copulation occurs within 30 min 75–80% of the time. If three or more males are present, copulation occurs only 5% of the time and average time until copulation averages 150 min [29]. This is due to increased intermale aggression and

possibly to mate preference, which is fairly common in older bitches. Male dogs may attempt mating several times in 1 day but more commonly breed once daily. It has been demonstrated that libido of male dogs suffers if they are used for breeding or have semen collected more than once daily [37]. Bitches will tolerate breeding more than once daily. The average bitch is in estrus for 9 days, but normal bitches may stand for as few as 3 days or as many as 21 days. Bitches may be bred by more than one male and will carry pups from different sires (superfecundation).

Queens should be brought to the male's territory for breeding. Territoriality is important to male cats and many will not breed away from their home. Queens in heat exhibit soliciting behavior by assuming the posture of lordosis, treading their hindlimbs and presenting their perineal area to the tom cat. The tom cat may show "caterwauling", a harsh, drawn-out cry that tells other males this is his territory and lets the queen know he is present. Usually the tom cries out softly just prior to mating. The tom cat grasps the scruff of the neck of the queen with his teeth. This grip does not break the skin and is not an aggressive act, but rather serves to stabilize the male and allow him to position the queen for copulation. Intromission and ejaculation last only seconds. Recorded time intervals for breeding in cats are 5–50 s for mounting and grasping of the neck by the male, 1–30 s for introduction of the penis and ejaculation, and 0–1 s for the male to dismount [38]. The queen cries out as ejaculation occurs, then immediately rolls over and bats at the male, who jumps away. The queen then goes through a period of frantic rolling and licking at her vulva, termed the after-reaction. The reason for the after-reaction is not known; some hypothesize it is a mechanism that promotes forward movement of spermatozoa. In a survey of 120 copulations, 54% of queens screamed when bred, 77% struck out at the tom immediately after breeding, 92% licked at their vulva and 100% rolled frantically [39]. Reported duration of the after-reaction is 1–7 min [38]. When the queen appears to have completed the after-reaction, the male will approach again. Domestic cats mated an average of about twice/hour in one study [40]. Most domestic cats breed 15 or fewer times in a day [41]. A single tom cat can service as many as 20 queens in a harem. Big cats may mate hundreds of times in 1 day, especially those species that are solitary by nature.

Length of estrus averages about 7 days in cats. Studies disagree as to whether or not being bred, and subsequently being induced to ovulate, decrease estrus length in domestic cats [39,42]. Estrus length is shorter in the fall, just prior to the end of the breeding season.

A phenomenon has been described in which cats that had been successfully bred went back into estrus during pregnancy and were bred again, creating kittens of very different age within the queen. This phenomenon, called superfetation, has never been proven to occur in domestic cats.

6. Abnormal mating behaviors of dogs and cats

6.1. Poor libido in males

Some male dogs are hesitant to breed bitches and rarely show investigative behavior (licking or sniffing at urine spots, flehmen, etc.). Proven causes for poor libido in male dogs

and cats include: (1) negative breeding experience (aggressive female, injury to the penis during mating, constant discipline for mounting behavior outside of breeding); (2) pain when attempting to mount or ejaculate (prostate disease, spinal or rearlimb orthopedic injury, hair rings in cats); (3) chromosomal abnormality (calico or tortoiseshell cat); (4) improper breeding environment (tom cat outside of his territory, area too busy); (5) mate preference (some dominant male dogs only will breed with the dominant bitch or only will breed females of their breed); and (6) improper age (too young or too old). A hypothesized cause for poor libido in animals is hyperprolactinemia, which is associated with poor libido in human males and females. Low serum testosterone concentration has never been reported as a cause of poor libido in animals, although some males will show more interest in females when treated with testosterone. Routine treatment with testosterone is not recommended; testosterone must be secreted in pulses for normal production of spermatozoa to occur and if you periodically provide the dog with a large amount of testosterone, you disrupt that pulsatile release and exert negative feedback to the pituitary, stopping secretion of LH and subsequent secretion of testosterone for an unpredictable length of time.

6.2. Inappropriate mounting/masturbation

Dogs and cats may occasionally exhibit inappropriate mounting and masturbation behaviors. Male dogs intended for breeding never should be excessively disciplined for mounting behavior because that may make them less willing to mount and breed bitches when you want them to. Castrated male cats that exhibit breeding behaviors may have a tumor of the adrenal gland that secretes testosterone. Male cats that have substantial amounts of testosterone in their system develop spines on their penis; examination of the penis for spines is a quick test for testosterone in male cats. Male dogs may exhibit mounting, extrusion of the penis and penile licking and inability to retract the penis into the prepuce (paraphimosis). If the dog is intact and is not intended for breeding, he should be castrated. If the dog is neutered, do not discipline him excessively as he may take that as positive reinforcement. Try to avoid conditions that cause the behavior, exercise him more, and teach him obedience commands and make him “sit” or “drop” when he starts to show the behavior. Treatment with progesterone-type drugs may lessen the behavior. Very occasionally, female dogs will show mounting and thrusting behavior. This probably is masturbation, as they stimulate the clitoris. Treatment is as described for male dogs.

6.3. Refusal of female to stand for breeding

Some females never show true standing behavior. Causes for this include: (1) dominant bitch; (2) physical abnormalities of the bitch or queen (vaginal stricture, spinal or rearlimb pain); and (3) improper breeding timing (bitch or queen not in estrus). Physical problems and improper breeding timing can be ruled out with a complete physical examination, including a digital vaginal examination in bitches, and by measures to determine optimal breeding timing, including measurement of progesterone in blood.

7. Maternal behaviors

7.1. Normal

7.1.1. Pregnancy

Bitches and queens do not exhibit any specific behaviors during pregnancy. They are not reported to get “morning sickness”, but many bitches will experience 7–10 days of inappetance about 3 weeks after breeding. Dogs and cats may get more particular about their diet when pregnant, but as far as we know they do not get cravings. With advanced pregnancy, as the enlarged uterus pushes on the stomach, bitches and queens eat smaller meals less frequently and become less active. Many have an increased respiratory rate or pant, again due to pressure from the enlarged uterus. Cats rarely pant and any open-mouth breathing in queens is cause for concern.

7.1.2. Nesting

Bitches and queens begin to exhibit nesting behavior about 1 week before giving birth. Most want to be in a secluded area but the occasional bitch or queen wants to be near the owner. Pick a spot for them or they will pick their own nest, invariably your closet or someplace else inconvenient. You want an area that is private but that can be observed easily and that can be cleaned. Commercial whelping and queening boxes are available. Children’s wading pools (dogs) and plastic dishpans (cats) work well, too. Some sort of nesting material that cannot be ingested by the dam and is easily laundered or replaced is recommended. Newspaper can be used, but may stain the neonates and dam. Towels work well. Feral cats often change nest sites, presumably to prevent predation of kittens [43]. Domestic cats given access to the entire house may do the same.

7.1.3. Parturition

Parturition is giving birth, termed whelping in dogs and queening in cats. Parturition is divided into three stages. Stage I labor is the long stage during which the cervix is dilating. The bitch or queen is uncomfortable and restless. She usually will not eat and may vomit. Bitches often pant. This stage may last up to 12 h in normal bitches and queens.

Stage II labor is passage of the offspring. Overt abdominal contractions are evident and the bitch or queen obviously is bearing down. Bitches and queens rarely cry out when giving birth. The puppy or kitten usually is passed within the amniotic sac. The bitch or queen bites through the amniotic membrane and vigorously licks the pup or kitten to stimulate breathing. Then the bitch or queen chews through the umbilical cord and pushes the pup or kitten beneath them. Puppies and kittens usually are passed every 15–60 min. In dogs, if a pup has not been passed in 2 h, veterinary intervention is recommended. However, normal queens may take a much longer time to pass all their kittens; in one survey, median queening time was 16 h, with a range of 4–42 h [39]. Bitches often tolerate the presence of humans they know well and some bitches seek out the owners at this stage. Queens like to be left alone and may stop labor if bothered too much.

Stage III labor is passage of the placentas. Stages II and III usually happen concurrently, with a bitch or queen passing one or two offspring, then some placentas, then some more offspring, etc. Bitches and queens often eat the placentas. This is an adaptation to keep the

den clean and prevent predation. However, the placentas offer no benefit to the bitch or queen and may cause gastroenteritis with vomiting and inappetance. Placentas should be removed unless the bitch or queen is excessively agitated by presence of a human.

7.1.4. *Care of offspring*

Most bitches and queens will not allow offspring to nurse until all have been born. Pups and kittens at birth are not capable of much movement, cannot control their own body temperature and must nurse within the first 8–12 h of life to ensure they get adequate nutrition, do not dehydrate and receive antibodies to protect them from disease. The suckling reflex is very strong in normal puppies and kittens and can be elicited easily. Puppies and kittens find the dam's nipples by trial and error and by olfaction. The bitch or queen may use her limbs to push the offspring into the area of the mammary glands. Queens often nearly form a circle while lying on their side, keeping the kittens warm and promoting their ability to suckle. While nursing, puppies and kittens knead the mammary gland; this may help promote milk letdown. Puppies generally do not show a preference for which mammary gland they use for nursing and are easily rotated so the owner can be sure that all pups get to nurse off the larger rear mammary glands that produce more milk. Kittens do show a preference for a specific nipple but queens generally make the same amount of milk from all mammary glands so this is not a concern. The bitch or queen should allow the offspring to nurse and should lick the genitals after feeding to stimulate urination and defecation; this behavior should continue until the pups or kittens are mobile, at about 3 weeks of age. Bitches and queens rarely leave the offspring for the first week postpartum, leaving only to eat and to urinate and defecate. By about 4 week, as the puppies and kittens become more mobile and their teeth start to erupt, the queen and bitch become more evasive, standing when the offspring attempt to suckle and leaving the offspring alone for longer periods of time.

Cross-fostering is placement of puppies or kittens with a dam that is not their own. This may be necessary because of disease or death of the dam or because the litter size is very large. Cross-fostering easily is accomplished in dogs and cats, both of which are species with natural tendencies to cross-foster. It appears that dams identify their offspring by olfaction, perhaps linked to release of oxytocin [44,45]. Cross-fostering is easiest if attempted in the first week of life and if the dam and surrogate dam are related.

Male dogs of domestic species virtually always ignore puppies. The very occasional male may attack pups but most do not seem to be aware of their existence. Similarly, domesticated male cats usually ignore kittens. Siamese males are reported to groom kittens of their breed on occasion. In some breeds of big cat, most notably the lion, an incoming male will kill the cubs in the pride and many of the females in the pride will then be induced to come into heat, ensuring the new male will get a chance to procreate. In domestic cats, loss of kittens is not consistently associated with the queen coming into heat, so there would not evolutionary advantage for tom cats to kill the kittens.

7.1.5. *False pregnancy*

False pregnancy, or pseudocyesis, is a normal phenomenon in bitches. At the end of diestrus, when progesterone concentrations fall and prolactin concentrations rise, the bitch exhibits mammary development, produces milk and may show behavioral changes as if she

is whelped including nesting and mothering of inanimate objects. Some bitches will be aggressive. This is most likely an evolutionary adaptation. In a pack of wild dogs, all females eventually cycle at the same time. The females low in the hierarchy in the pack may not be bred. If they go through false pregnancy and are lactating at the same time as related females that have given birth, they can cross-foster the pups and in that way ensure their genetics are carried on.

7.2. Abnormal behavior

7.2.1. Aggression of the dam

Postpartum aggression is uncommon in queens. In bitches, postpartum aggression can occur and may be unassociated with premonitory signs. Aggression may be exacerbated by vocalization of pups. Mild sedation occasionally is necessary to ensure safety of humans and other animals in the household. All bitches showing aggressive behavior should be seen by a veterinarian to ensure their behavior does not reflect pain, for example, from mastitis.

7.2.2. Savaging/cannibalism of offspring

The occasional bitch or queen will cannibalize their offspring. This behavior also is called *kronism*. In bitches, causes include pain (usually associated with mastitis) and eclampsia. Cannibalism is more common in cats and has been reported to account for 12.5% of kitten deaths prior to weaning [41]. Causes include pain, too large a litter, stress and overcrowding. Occasionally queens will kill kittens from other females in a facility; it is thought this is a predator–prey response since they do not recognize those kittens as their own and kittens are the size of prey.

7.2.3. Rejection of offspring

Some bitches and queens reject their offspring. If only one or two offspring are repeatedly pushed away from the nest or carried away and hidden, this suggests there is something wrong with that puppy or kitten and it should be examined by a veterinarian. Bitches and queens routinely reject offspring that are cold or are not active. If the entire litter is being rejected, that suggests something is wrong with the queen. Things to look for are signs of disease in the dam (mastitis, metritis, eclampsia) and environmental factors that may be stressing the dam (overcrowding, large litter). Some dams are poor mothers for their first litter, especially if they are a “high-strung” animal. Many of these dams go on to be good mothers with subsequent litters.

References

- [1] Valros A, Rundgren M, Spinka M, et al. Oxytocin, prolactin and somatostatin in lactating sows: associations with mobilisation of body resources and maternal behavior. *Livestock Prod Sci* 2004;85:3–13.
- [2] Whitman DC, Albers HE. Role of oxytocin in the hypothalamic regulation of sexual receptivity in hamsters. *Brain Res* 1995;680:73–9.
- [3] Hammond MG. In: Management of hyperprolactinemia; 1991.p. 19–23.
- [4] Kruger THC, Haake P, Hartmann U, et al. Orgasm-induced prolactin secretion: feedback of control of sexual drive? *Neurosci Biobehav Rev* 2002;26:31–44.

- [5] Mong JA, Pfaff DW. Hormonal and genetic influences underlying arousal as it drives sex and aggression in animal and human brains. *Neurobiol Aging* 2003;24:583–8.
- [6] Michael RP. Estrogen-sensitive neurons and sexual behavior in female cats. *Science* 1962;136:322–3.
- [7] Warembourg M, Leroy D. Comparative distribution of estrogen receptor alpha and beta immunoreactivities in the forebrain and the midbrain of the female guinea pig. *Brain Res* 2004;1002:55–66.
- [8] Jones JE, Pick RR, Wade GN. Food deprivation inhibits estrous behavior in hormone-treated Syrian hamsters despite elevated estradiol levels. *Horm Behav* 2002;41:316–20.
- [9] Jones JE, Wade GN. Acute fasting decreases sexual receptivity and neural estrogen receptor alpha in female rats. *Physiol Behav* 2002;77:19–25.
- [10] Henry LA, Witt DM. Resveratrol: phytoestrogen effects on reproductive physiology and behavior in female rats. *Horm Behav* 2002;41:220–8.
- [11] Auger AP. Steroid receptor control of reproductive behavior. *Horm Behav* 2004;45:168–72.
- [12] Schumacher M, Coirini H, Robert F, et al. Genomic and membrane actions of progesterone: implications for reproductive physiology and behavior. *Behav Brain Res* 1999;105:37–52.
- [13] Jochle W, Jochle M. Reproductive and behavioral control in the male and female cat with progestins: long-term field observations in individual animals. *Theriogenology* 1975;3:179–85.
- [14] Temple JL, Scordalakes EM, Bodo C, et al. Lack of functional estrogen receptor beta gene disrupts pubertal male sexual behavior. *Horm Behav* 2003;44:4270–434.
- [15] Schulz KM, Richardson HN, Zehr JL, et al. Gonadal hormones masculinize and defeminize reproductive behaviors during puberty in the male Syrian hamster. *Horm Behav* 2004;45:242–9.
- [16] Pereira OCM, Coneglian-Marise MSP, Garardin DCC. Effects of neonatal clomiphene citrate on fertility and sexual behavior in male rats. *Comp Biochem Phys A Mol Integrat Phys* 2003;134:545–50.
- [17] Carter CS. Developmental consequences of oxytocin. *Physiol Behav* 2003;79:383–97.
- [18] Withuhn TF, Kramer KM, Cushing BS. Early exposure to oxytocin affects the age of vaginal opening and first estrus in female rats. *Physiol Behav* 2003;80:135–8.
- [19] Koyama S. Primer effects by conspecific odors in house mice: a new perspective in the study of primer effects on reproductive activities. *Horm Behav* 2004;46:303–10.
- [20] Goodwin M, Gooding KM, Regnier F. Sex pheromone in the dog. *Science* 1979;203:559–61.
- [21] Wirant SC, McGuire B. Urinary behavior of female domestic dogs (*Canis familiaris*): influence of reproductive status, location, and age. *Appl Anim Behav Sci* 2004;85:335–48.
- [22] Ranson E, Beach FA. Effects of testosterone on ontogeny of urinary behavior in male and female dogs. *Horm Behav* 1985;19:36–51.
- [23] McNutt JW. Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Anim Behav* 1996;52:1067–77.
- [24] Borchert PL. Aggressive behavior of dogs kept as companion animals: classification and influence of sex, reproductive status and breed. *Appl Anim Ethol* 1983;10:45–61.
- [25] Wright JC, Nesselrode MS. Classification of behavior problems in dogs: distributions of age, breed, sex and reproductive status. *Appl Anim Behav Sci* 1987;19:167–78.
- [26] Pal SK, Ghosh B, Roy S. Agonistic behaviour of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. *Appl Anim Behav Sci* 1998;59:331–48.
- [27] Daniels TJ. The social organization of free-ranging urban dogs. I. Non-estrous social behavior. *Appl Anim Ethol* 1983;10:341–63.
- [28] Daniels TJ. The social organization of free-ranging urban dogs. II. Estrous groups and the mating system. *Appl Anim Ethol* 1983;10:365–73.
- [29] Beaver B. Canine behavior: A guide for veterinarians. Philadelphia: WB Saunders Co., 1999.
- [30] O'Farrell V, Peachey E. Behavioural effects of ovariectomy on bitches. *J Sm Anim Pract* 1990;31:595–8.
- [31] Hopkins SG, Schubert TA, Hart BL. Castration of adult male dogs: effects on roaming, aggression, urine marking, and mounting. *J Am Vet Med Assoc* 1976;168:1108–10.
- [32] Nielson JC, Eckstein RA, Hart BL. Effects of castration on problem behaviors in male dogs with reference to age and duration of behavior. *J Am Vet Med Assoc* 1997;211:180–2.
- [33] Hart BL. Effect of gonadectomy on subsequent development of age-related cognitive impairment in dogs. *J Am Vet Med Assoc* 2001;219:51–6.

- [34] Raymer J, Wiesler D, Novotny M, et al. Chemical scent constituents in urine of wolf (*Canis lupus*) and their dependence on reproductive hormones. *J Chem Ecol* 1986;12:297–314.
- [35] VanderHorst VGJM, Holstege G. Sensory and motor components of reproductive behavior: pathways and plasticity. *Behav Brain Res* 1998;92:157–67.
- [36] Beach FA. Coital behavior in dogs: IX. Sequelae to ‘coitus interruptus’ in males and females. *Physiol Behav* 1970;5:263–4.
- [37] Taha MB, Noakes DE, Allen WE. The effect of the frequency of ejaculation on seminal characteristics and libido in the beagle dog. *J Sm Anim Pract* 1983;24:309–15.
- [38] Lein D, Concannon PW, Hodgson BG. Reproductive behavior in the queen. *J Am Vet Med Assoc* 1982;181:275.
- [39] Root MV, Johnston SD, Olson PNS. Estrous length, pregnancy rate, gestation and parturition lengths, litter size, and juvenile mortality in the domestic cat. *J Am Anim Hosp Assoc* 1995;31:429–33.
- [40] Concannon P, Hodgson B, Lein D. Reflex LH release in estrous cats following single and multiple copulations. *Biol Reprod* 1980;23:111–7.
- [41] Beaver B. Feline behavior: A guide for veterinarians. Philadelphia: WB Saunders Co., 1992.
- [42] Wildt DE, Charman Guthrie S, Seager SWJ. Ovarian and behavioral cyclicity of the laboratory maintained cat. *Horm Behav* 1978;10:251–7.
- [43] Feldman HN. Maternal care and differences in the use of nests in the domestic cat. *Anim Behav* 1993;45:13–23.
- [44] Levy F, Keller M, Poindron P. Olfactory regulation of maternal behavior in mammals. *Horm Behav* 2004;46:284–302.
- [45] Engelmann M, Ebner K, Wotjak CT, et al. Endogenous oxytocin is involved in short-term olfactory memory in female rats. *Behav Brain Res* 1998;90:89–94.